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Reynolds, R. T., and S. M. Joy. 1998. Distribution, Territory Occupancy, Dispersal, and Demography of Northern Goshawks on the Kaibab Plateau, Arizona. Final Report, Arizona GF Heritage Project, No 194045. 76pp.

Distribution, Territory Occupancy, Dispersal, and Demography of Northern Goshawks on the Kaibab Plateau, Arizona

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Final Report for

Arizona Game & Fish
Heritage Project No. I94045

31 January 1998

This project was cooperatively funded by the

USDA, Forest Service, Region 3
USDA, Forest Service, Rocky Mountain Research Station, and
Arizona Game & Fish

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ABSTRACT: We studied 347 nesting attempts on 107 nesting territories of northern goshawks (*Accipiter gentilis*) on 1,732 km^2 of the Kaibab Plateau, Arizona from 1991-1996. Mark and recapture methodology was used to estimate survival probabilities, territory and mate fidelity, turnover on territories, and dispersal. Territories were regularly spaced at a mean nearest-neighbor distance of 3.88 km (n = 100, P = 0.98, Cramer-von-Mises). An estimate of the total breeding population on the study area (146 territories) suggested that about 73 percent of the breeding population was located during the study. Annual proportion of pairs that laid eggs, production of fledglings, nesting success, fecundity, and recapture rates varied from highs in 1991-1993 to a low in 1994; there was partial recovery in these parameters in 1995 and 1996. Declines appeared to be associated with variation in abundance of several prey species, especially the red squirrel (*Tamisciurus hudsonicus*).

Territory and mate fidelity was high for both sexes, but territory fidelity of males (91.7 %) exceeded that of females (78.6 %); two males and five females changed territories during the study and none retained their mates in these moves. Only one case of divorce (both hawks confirmed alive in subsequent years) was recorded. Mean breeding dispersal distances were slightly greater for females (5.2 km, SD = 2.66) than for males (2.8 km, SD = 1.06); in all cases, both sexes moved to territories either adjacent to their original territory or two territories distant. Natal dispersal distances also tended to be greater in females ($\bar{x}$ = 21.5 km, SD = 9.18) than males ($\bar{x}$ = 15.9, SD = 6.48). Males were an average one year older than females when first found breeding. Overall annual replacement (turnover) rates of breeding hawks on territories was 32 percent, with males being replaced at a higher rate (42 %) than females (25 %).

Six of 256 nestlings banded during the study were recaptured in subsequent years -- too few to estimate survival rates for juveniles. All hawks aged ≥ 1-year-old when first captured were pooled into a non-juvenile age class for survival estimation. Goodness-of-fit tests on the capture-recapture data from non-juveniles in program RELEASE (Pollock et al. 1985, Burnham et al. 1987) indicated the appropriateness of Cormack-Seber-Jolly open population models for estimating survival and recapture rates. Of 64 capture-recapture models examined in program

SURGE (Pollock et al. 1990, Lebreton et al. 1992, Burnham et al. 1995), the most parsimonious (lowest AIC values) model $\{Phi_s, P_t\}$ showed that while survival differed between the sexes, it was constant for each sex during the study period (males = 0.688, SE = 0.062; females = 0.866, SE = 0.051). Estimates of recapture probabilities from the model with the best fit to the data showed that recapture rates varied with time but not sex, and ranged annually from 0.149 (1994) to 0.662 (1992). Time effects on recapture rates corresponded with the variable proportions of goshawk pairs laying eggs each year -- for the most part only nesting hawks were captured.

Lambda (λ) could not be estimated for the population because we were unable to determine the survival rates of the juvenile age class. Estimates of juvenile survival required to maintain a stable population (i.e, $\lambda = 1$), given the adult survival and fecundity rates determined during the study period, were 0.305 for females and 0.709 for males. The survival rate for juvenile females is similar to rates in other raptors, but the required rate for juvenile males is unrealistic and may reflect an artificially low estimate of survival of adult males due to an insufficient number of adult males included so far in the capture-recapture study and/or too few recapture occassions.

Regular spacing of territories at shorter nearest-neighbor distances then reported elsewhere for goshawks and the high annual rate of occupancy of territories by hawks suggested that the Kaibab goshawk population was saturated. Some evidence also suggested the population was relatively stable: 1) low recruitment rate and age of hawks when first recruited into the breeding population suggested that most territories were already occupied and young hawks had to wait for years before a territory became available, and 2) high fidelity of both adult sexes to territories suggested that other breeding areas on the Kaibab were occupied and not available; if a hawk abandoned a territory it might not find an available territory and therefore lose its own. Not all territories were equal, however, in numbers of years in which the territorial pair nested and numbers of young produced.

Adequate methods and sampling levels are necessary for accurate estimates of demographic variables and identifying population trends in avian monitoring programs. Minimum number of

nesting pairs needed in a goshawk monitoring program to accurately estimate means and standard errors of annual number of fledglings produced per nest and proportion of active nests that were successful was 35-40 pairs. However, minimum number of territories needed to estimate the annual proportion of pairs laying eggs, a critical variable in estimating fecundity, was 80-90. Estimating nest density required intensive, systematic searches of large areas for nests of goshawks, and searches should be repeated over years to detect pairs that do not breed every year. After a sample of territorial pairs has been identified, monitoring programs whose objectives include nest productivity, nesting success, fecundity, and nest density require about five persons per 40 territories and between 10-13 persons per 80 territories.

Key Words: *Accipiter gentilis*, Arizona, capture-recapture, demography, dispersal, fecundity, forest management, Kaibab Plateau, nesting success, northern goshawk, reproduction, spatial distribution, adult and juvenile survival, turnover, territory and mate fidelity, territory occupancy.

INTRODUCTION

The northern goshawk (*Accipiter gentilis atricapillus*) is the largest member of the genus *Accipiter* in North America. Like other members of the genus, goshawks are morphologically and behaviorally adapted to hunt for birds and mammals in forests and woodlands. Their short wings and long tails provide maneuverability for capturing prey in forests and their short perch-short flight foraging tactics (Kenward 1982) are suited for prey searching in environments where their visual field is impaired by dense vegetation (Reynolds et al. 1992). Goshawks breed in nearly all forest and woodland types found within their geographic range; even open habitats such as shrub and tundra communities, where riparian trees or small forest patches provide nest sites, are sometimes used (White et al. 1965, Swem and Adams 1992, Younk and Bechard 1994). In spite of wide differences in the species composition and structure of occupied vegetative communities, forest stands in which goshawks place their nests have a high degree of structural similarity; nest sites are typically composed of large trees with relatively high canopy cover and open understories (Reynolds et al. 1982, Moore and Henny 1983, Spieser and Bosakowski 1987, Hayward and Escano 1989). Radio-telemetry studies showed that goshawks forage in a wide range of forest structures but spend a disproportionate amount of time in mature-to-old forests (Widén 1989, Bright-Smith and Mannan 1994, Hargis et al. 1994). Use of older forests by hunting goshawks might be related to the openness of old forest understories where goshawks can detect and capture prey and, because old forests are the prime habitats of many goshawk prey species, prey abundance may be greater there (Reynolds and Meslow 1984, Reynolds et al. 1992).

Recent research has focused on the effects of forest management on the viability of goshawk populations (Block et al. 1994). Many studies were of short duration and did not include pre- and post-management responses of goshawks. In addition, management of many forest districts typically occurs in small, widely dispersed annual treatments that result in relatively slow rates of habitat change at landscape-scales, at least within the time frame of most goshawk studies. Studies at large spatio-temporal scales, which include many goshawk territories and sufficient years to detect responses of goshawk populations to slow rates of habitat change from natural fluctuations (e.g., weather, prey populations), are needed.

Habitat change may affect the stability of populations by altering survival probabilities and fecundity. Yet, while counts of goshawks might appear stable over time, the stability may only result from immigration on to the area. Detection of responses of goshawk populations to management requires estimates of population size and other fundamental demographic variables such as birth, immigration, mortality, and emigration rates. Capture-recapture models can be used to estimate these variables, as well as discriminate between populations that appear stable due to immigration from one that is inherently stable due to a balance between births and deaths (Raphael et al. 1996).

We report on the distribution of nesting pairs, annual proportion of pairs laying eggs, nesting success, fecundity, fledgling sex ratio, mate and territorial fidelity, and natal and breeding dispersal of goshawks on the Kaibab Plateau in northern Arizona. Estimates of annual survival rates of goshawks in this population based on mark-recapture methodology are also provided. We identify annual variation in several of these demographic variables and discuss some of the possible sources underlying the variation on the Kaibab Plateau. In the interest of monitoring goshawk populations in managed landscapes, we provide estimates of the minimum number of goshawk territories and pairs of hawks that need to be included in a monitoring program to accurately determine annual territory occupancy rates, production of fledglings, and nesting success in an analysis of these variables from of the Kaibab goshawk population. Finally, we estimate the required survival rates of juvenile goshawks under the condition that the Kaibab population remains stable ($\lambda = 1$) given our estimates of adult survival and fecundity.

STUDY AREA

The 1,732 km^2 study area on the Kaibab Plateau in northern Arizona includes all of the Plateau above 2,182 m elevation. The study area includes both the North Kaibab Ranger District (NKRD) of the Kaibab National Forest (KNF) and the Grand Canyon National Park (GCNP), and is largely covered by ponderosa pine (*Pinus ponderosa*), mixed-conifer, and spruce/fir (*Picea engelmannii-Abies lasiocarpa*) forests.

The Kaibab Plateau is an oval-shaped (95 km x 55 km), limestone plateau that rises from a shrub-steppe plain at 1750 m elevation to its highest point at 2800 m, and is dissected by moderately sloping valleys (Rasmussen 1941). The Plateau is bounded by escarpments of the Grand Canyon of the Colorado River on its southern side, and by steep slopes on the east and gentle slopes on the north and west sides that descend to the plain. Pinyon (*Pinus edulis*)-juniper (*Juniperus* spp.) woodlands occur below the study area at elevations between 1830 and 2075 m. Ponderosa pine forests (about 122,400 ha) occur between 2075 to 2450 m, mixed-conifer forests (about 51,600 ha) between 2450 to 2650 m, and spruce-fir forests (about 30,600 ha) from 2650 to 2800 m (Rasmussen 1941, White and Vankat 1993) (Fig. 1). At the transition between forest types, there typically is an elevation range where, because of slope and aspect differences, adjacent forest types intermix. There is a series of narrow meadows on top of the Kaibab Plateau containing grasses and herbaceous vegetation. Annual precipitation on the Kaibab Plateau averages 67.5 cm, with winter snowpacks of 2.5-3.0 m (White and Vankat 1993). Winters are cold and summers are cool. A drought period typically occurs in May and June, followed by a mid- to late-summer monsoon season with frequent (2-4 per week) thunderstorms and heavy showers.

Forests in the ponderosa pine type were the most open forest types on the study area. This type was dominated by ponderosa pine, but had components of pinyon pine and Utah juniper (*Juniperus utahensis*) in the lower half, and quaking aspen (*Populus tremuloides*) at higher elevations. Understories consisted primarily of grasses, mainly *Poa fenderiana, Sitanion hystrix,* and *Muhlengergia montana* (Rasmussen 1941, Merkle 1962). Common understory shrubs were *Ceanothus fenderli, Robinia neomexicana, Odostemon (=Berberis) repens, Sambucus caerulea, Ribes inebrians, Chrysothamus parryi, Sericotheca glabrescens, Symphoricarpos sp., and*

Arctostaphylos patula. Quercus utahensis, Amerlanchier, and Cowania stansburiana are abundant only in lower elevations of the pine zone (Rasmussen 1941).

The mixed-conifer forest on the Kaibab Plateau contained a diversity of tree species whose proportional mixing in a stand depended on elevation and topographic position. White and Vankat (1993), using basal area dominance of tree species in the GCNP on the Plateau, recognized four mixed conifer forest types, and we found approximate representatives of these mixed conifer types on the NKRD. These included the *PINUS PONDEROSA - PSEUDOTSUGA MENZIESII* type, with relatively open canopies and understories dominated by ponderosa pine, especially in the larger size classes, but with some co-dominance of Douglas-fir in the canopy. White fir and quaking aspen were limited to the smaller size classes (White and Vankat 1993). Common understory plants included *Muhlenbergia montana, Carex siccata, Lotus foenea, Rosa arizonica, Berberis repens, Antennaria aprica,* and *Fragaria ovalis* (White and Vankat 1993). This forest type occurred on dry, warm ridgetops and steep south, southeast, and southwest exposures up to 2600 m asl (White and Vankat 1993). The *PINUS PONDEROSA - ABIES CONCOLOR* type had greater canopy and understory cover. White fir was abundant, but had a lower basal area than ponderosa pine, and was especially abundant in the small and medium size classes. Understories species were *Muhlenbergia montana, Carex siccata, Lotus utahensis, Achillea lanulosa, Rosa arizonica, Berberis repens, Antennaria aprica,* and *Fragaria ovalis* (White and Vankat 1993). This forest type occurred on gentle, southern exposures, flat ridgetops, and on steep eastern and western exposures up to 2700 m asl (White and Vankat 1993). The *PICEA PUNGENS - PINUS PONDEROSA* type had low-to-medium canopy cover and high understory cover. Blue spruce was dominant with highest basal area, followed by quaking aspen and ponderosa pine. Blue spruce was represented in all size classes, while ponderosa pine was mainly in the medium-to-large size classes. Quaking aspen was important in the intermediate size classes, and white fir and subalpine fir were abundant in the smaller size classes. Common understory plants were *Muhlenbergia montana, Lotus utahensis, Achillea lanulosa, Rosa arizonica, Castillea lanulosa,* and *Fragaria ovalis* (White and Vankat 1993). This forest type occurred on lower slopes near meadow edges and on middle and lower slopes with eastern and western exposures up to 2700 m asl (White and Vankat 1993). The *ABIES CONCOLOR - PINUS PONDEROSA - PSEUDOTSUGA MENZIESII* type had a high canopy cover and sparse understory cover. White fir was dominant and ponderosa pine and Douglas-fir was intermediate. Each of these species was co-dominate in the large size classes, but white fir was most abundant in the smallest classes. Common understory species were *Berberis repens, J. communis, Poa fenderleriana, Sitanion hystrix, Carex foenea*, *Achillea lanulosa, Pedicularis centranthera,* and *Pryola virens* (White and Vankat 1993). This forest type occurred on middle and upper gentle slopes with eastern, southern, and western exposures and flat ridgetops up to 2700 m asl (White and Vankat 1993).

The spruce-fir forest type had the highest canopy cover and lowest understory cover of forest types on the Plateau. Engelmann spruce was dominant in the number of trees and basal area, and was well represented in all size classes. Subalpine fir was co-dominant with intermediate basal area and high density, especially in the intermediate-to-small size classes. Ponderosa pine was a common tree, especially on warmer and drier sites, where it occurred in the older-age classes. Quaking aspen had intermediate basal area and number of trees, and was most abundant in the intermediate and small size classes; there were sparse to moderate levels of Douglas-fir, white fir, and blue spruce, and there was little shrubby and herbaceous cover (Merkle 1962, White and Vankat 1993). Below 2,500 m asl, this forest type occurred only on steep, north and east slopes and narrow valleys (Merrkle 1962, White and Vankat 1993). Understory species were *Berberis repens, J. communis, Sitanion hystrix, Achillea lanulosa, Ligusticum porteri, Fragaria ovalis,* and *Pyrola virens* (White and Vankat 1993).

In 1893 the Grand Canyon Forest Reserve, which included the Kaibab Plateau and the South Rim, was established. GCNP was established in 1919 and included the southern third of the Kaibab Plateau south of the NKRD. The Kaibab Plateau was spared the extensive logging that occurred elsewhere on the Colorado Plateau and Southwest during the railroad logging era (late 1800's-early 1900's), primarily because of its isolation from southern rail heads on the south side of the Grand Canyon (Pearson 1950, J. Hanson pers. comm.).

Organized tree harvests on the NKRD did not begin until the early 1920's and until the 1960's, tree cutting was limited to dead and dying trees (sanitation cuts) (Burnett 1991). In the late 1960's clear-cutting began in mixed-conifer forests but was discontinued in the early 1970's (total cut = 922 ha); single tree cutting in ponderosa pine continued through the mid-1980's. Intensive management at the forest stand level began in the mid-1980's with even-aged silvicultural treatments in the pine and mixed-conifer forests and continued until 1991. From the 1940's to 1990, the total volume of wood removed from the NKRD increased by a factor of five, from 9077 to 48,412 boardfeet per ha (1992 Kaibab National Forest Timber Atlas, J. Ellenwood, pers. comm.). While early sanitation cutting occurred over much of the NKRD, the application of stand-level management beginning in 1986 resulted in a reduction of the total area harvested (1986-1991) to 12,632 ha (1992 Kaibab National Forest Timber Atlas, J. Ellenwood, pers. comm.).

Extensive livestock grazing began in 1885-86 and continued until the mid 1900's, except in the GCNP where it likely ceased in 1919 (Rasmussen 1941, Merkle 1962). Predator control in the 1920's may have resulted in an enlarged deer population and subsequent overgrazing in the 1920's, 1930's, and 1950's (Rasmussen 1941, Merkle 1962). Reduction of ground fuels by grazing, increased discontinuity of fuels resulting from road construction, and suppression of fires on the Kaibab Plateau, which began in the early 1900's, resulted in the reduction of historically frequent, low-severity surface fires (Rasmussen 1941, White and Vankat 1993). Frequent, low intensity fires maintained ponderosa pine and some mixed-conifer forests in open tree conditions. Frequent fires also favored fire-tolerant species like ponderosa pine and Douglas-fir. White fir, a fire intolerant species, was less abundant in the canopy (White and Vankat 1993). On the Plateau, fire suppression has resulted in an increase in the number of sapling and pole-sized ponderosa pine and white fir by a factor of almost eight in ponderosa pine forests and by 11 (mostly white fir) in mixed-conifer forests (1992 Kaibab National Forest Timber Atlas, J. Ellenwood, pers. comm.).

Although mixed-conifer and spruce-fir forests on the Kaibab Plateau naturally burned less frequently, fires affected the composition and structure of these forests through differences in the degree of fire- and shade-tolerance among tree species (Rasmussen 1941). The presence of ponderosa pine and Douglas-fir in only the largest size classes on many mixed-conifer and spruce/fir sites on the Kaibab Plateau suggest the lack of fire is changing the composition in these forests. Some of these changes may affect the distribution and abundance of goshawks by altering the composition and abundance of prey resources.

METHODS

Field Methods

A "nesting territory" is an area used by a single pair of goshawks during the nesting season. While sizes of goshawk territories were unknown, in some areas nests in adjacent territories were spaced at 3.0 to 5.6 km (Reynolds and Wight 1978, Reynolds et al. 1994). Goshawk territories typically contain multiple alternate nests, generally in the central portion of territories, used by the resident goshawks over years (Reynolds et al. 1994). An "occupied territory" is a territory in which a pair or single hawk has been observed on two or more occasions, usually in the vicinity of a historic nest, in a breeding season; the hawk's presence is typically coupled with abundant feces, molted feathers, or fresh construction on a nest. "Traditional territories" are occupied territories found in prior years; the occupancy and reproductive status of traditional territories could, therefore, be monitored throughout a current breeding season. An "active nest" is a nest in which eggs were laid, and "failed nests" are nests in which eggs or nestlings were lost (= no nestlings fledged). "Nest area" is a 15-20 ha area surrounding a nest that typically includes prey plucking sites and tree-roosts of the adult goshawks. A nest area may contain one or more alternate nests. Most territories have several nest areas.

In 1991, we began searches for goshawk nests in the northwest portion of the Kaibab Plateau. In subsequent years (1992-1996), nest searches were expanded toward the north, east, and south, resulting in an annual expansion of the study area. By the close of the 1996 breeding season, about 80 percent of the Plateau had been searched; only the extreme south and southeast portion of the Plateau had not received searches. Nest searches were conducted by systematically searching large areas (1,600-2,400 ha) for goshawk nests (Reynolds 1982) and by broadcasting goshawk vocalizations from predetermined broadcast stations on transects in 2,400-4,800 ha areas using procedures and a broadcast-station distribution described by Joy et al. (1994) and Kennedy and Stahlecker (1993). Each year nest searching began in April and ended after the post-fledging dependency period (August).

Each spring, all nests used by goshawks in prior years were visited in attempts to determine the occupancy status of territories. If goshawks were not using a "historic" nest within a territory, foot searches (Reynolds 1982) were conducted within 800 m radii centered on the most recently-used nest within a territory. If an active nest was not located during foot searches, areas of 1,500 m radii were broadcasted as described above.

Visits to nests during a breeding season were made on a weekly basis to determine the status of nesting attempts and to trap, band, or resight breeding adults. Nests were climbed 1 to 2 times during the nestling period to determine the number of young, causes of nest failure, and to band nestlings. In studies with seasonal nest searches, nesting success is often overestimated because nests failing early in a season are less likely to be detected than successful nests (Steenhof and Kockert 1982). To control for this, we determined annual nesting success only for territories discovered in a prior year (= traditional territories). Thus, a year's nesting success was only determined for those nests where monitoring began at or near egg laying. We compared annual estimates of nesting success from traditional territories to annual estimates determined with the Mayfield (1961) method. The Mayfield method estimates nesting success based on "days of exposure" and daily nest survival rates from all breeding attempts checked twice or more during a nesting season, regardless of when in a breeding season nests were found. "Mayfield visits" to nests were made weekly in 1992-1996. Beginning and ending dates of incubation and nestling periods were determined by back- and fore-dating from ages of nestlings (Boal 1994) and known dates of egg laying, hatching, and fledging. Average dates were determined for egg laying, hatching, and fledging each year. Days of exposure were calculated using a 32-day incubation period and a 35-day nestling period (Reynolds and Wight 1978). Standard errors of the Mayfield estimates of nesting success were calculated after Johnson (1979).

Nesting adults were trapped in nest areas with dho-gaza traps arranged in a "V" around a live great horned owl (*Bubo virginianus*) during the nestling and fledgling stages (Bloom 1987), or with "falling-end" Swedish goshawk traps (Kenward and MarcstrÖm 1983) baited with domestic pigeons (*Columba livia*) and placed in nest areas or along "trap-lines" away from nests. The age (juvenile = 0 years, adult 1 = 1 year, adult 2 = 2 years, adult 3≥ 3 years) of goshawks was determined by plumage, and its sex by behavior prior to capture and morphometrics (Reynolds et al. 1994). Fledglings were captured during the last two weeks of the nestling period by climbing to nests. Adults and fledglings were weighed, measured, and fitted with USFWS aluminum leg bands and colored leg bands with unique 2-character alpha-numeric codes that were readable to 50-80 m with 20-40 power spotting scopes (Reynolds et al. 1994). Nestlings were sexed on the basis of body mass and tarus-metatarsus length.

Locations of nest trees were determined using a global positioning system (GPS: Trimble Navigation Ltd. 1992, 1994). GPS coordinates for each nest tree were generated in the Universal Transverse Mercator (UTM) projection and verified using field plots, topographical knowledge, and site visits. Digital elevation models (DEMs) of 32 7.5-min USGS quadrangles were latticed together in a geographical information system (GIS) to produce an single DEM of the Kaibab Plateau.

Data Analysis

We used UTM coordinates from GPS-determined locations of all nests and ARC INFO (ESRI) to calculate distances between alternate nests within territories, nearest-neighbor distances among nests of adjacent pairs of hawks, and natal and breeding dispersal distances. Mean distances between alternate nests within territories were calculated as the mean of distances among all possible combinations of alternate nests within a territory (e.g., nest A-B, B-C, C-A). The nearest-neighbor distances among nests of adjacent pairs of hawks was calculated as distances between geometric centroids of territories, where territory centroids were the geographic mean of coordinates between alternate nests in a territory (generated in ARC/INFO, ESRI 1991). The geographic mean was weighted by the number of times a given nest was used; if a nest was used during 2 years in the study and another during one year, the centroid was closer to the nest used twice. In territories in which only one nest was used, the single nest was the centroid for that territory. Nearest-neighbor distances between territory centroids were calculated with and without duplicate measures between reciprocal nearest-neighbors (Diggle 1983). Nearest-neighbor distances, measured with duplicate measures between reciprocal nearest pairs in a population, provides estimates of a minimum average distance between individuals (Diggle 1983). Nearest-neighbor distance without duplicate measures between reciprocal pairs provides a more realistic estimate of territory spacing because more of the actual variability in spacing of neighbors is taken into account.

Ripley's K function (Ripley 1981, S-Plus 1995) was used to model the distribution of 100 territory centroids (excluding 4 centroids in southeastern GCNP where searches had been incomplete). This procedure counts centroids that fall within a designated distance of each centroid to provide a measure of dispersion, corrected for edge effects (Cressie 1991). Observed counts [L(t)] were plotted against the distances at which the counts were made and compared with 95% dispersion (confidence) envelopes estimated from 100 populations of 100 points simulated under complete spatial randomness ("CSR" process). Data below the envelopes reflect regular ["Simple Sequential Inhibition" (SSI)] spacing, within the envelopes reflect random spacing, and data above envelopes reflect aggregated spacing ("Neyman-Scott"). We modeled the K function of centroids to 15,000 m to capture all possible inter-territory distances.

The Cramer-von-Mises goodness-of-fit statistic (Cressie 1991) was used to test the null hypothesis that the data came from a CSR process at the $\alpha = 0.05$ level. Rejection of the null required fitting the data to the alternative K function of a regular (Pielou 1960, Strauss 1975) or aggregated process (Neyman and Scott 1957) and comparing the centroids' distribution against the appropriate simulation envelope. Alternate distributions were followed by a Cramer-von-Mises goodness-of-fit (Cressie 1991) test of suitability of the alternate process. All spatial analyses were performed using S-Plus (1995) and the spatial library developed for S-Plus by Reich and Davis (1996).

Territory fidelity is the occupancy, in subsequent breeding seasons, of the same territory by the same hawk, or pair of hawks. We tallied territory infidelity only when hawks that abandoned a territory were found alive in the year of abandonment, or in subsequent years. Mate fidelity is the retention of the same mate in two or more breeding seasons. Mate infidelity (divorce sensu Rowley 1983) was tallied only when both members of a pair were found in subsequent breeding seasons to be paired with different mates, or when one mate was paired with a new mate and its original mate was found alive in subsequent years. Turnover is the replacement of a marked goshawk that nested on a territory in a previous breeding season by a new hawk in a current season. A hawk may be replaced on a territory due to its death, breeding dispersal, or expulsion by another hawk. "Turnover opportunities" were cases where the identities of a male or female on a territory was known in consecutive years.

The demographic design of this study consisted of capturing, banding, and releasing nesting goshawks, and then recapturing or resighting them in subsequent breeding seasons. Age, sex, and reproductive status of individuals were determined as described above. We used field counts of the number of young in nests within the two weeks of fledging as estimates of productivity and fecundity. July 15, the average date of fledging among all years, was considered the date of "birth." All nests were visited within 14 days prior to fledging to band and count nestlings. Number of young produced per nest was the number of young counted during that 14-day period. For nests found late in a breeding season (mostly in new territories), productivity was estimated by counting fledged young during the post-fledgling dependency period.

The capture-recapture history of individual goshawks provided the basis for parameter estimation and hypothesis testing in capture-recapture analysis of survival. Capture is defined as the capturing or resighting (reading a hawk's alpha-numeric color band from a distance) of individual goshawks. Estimates of annual survival rates were calculated using Cormack-Seber-Jolly open population models in Program SURGE (Pollock et al. 1990, Franklin et al. 1996). Akaike's Information Criterion (AIC) was used to identify models that best fit the data (Akaike 1973, Burnham and Anderson 1992, Anderson et al. 1994, Franklin et al. 1996). Goodness-of-fit tests (Tests 1-3 in Program RELEASE) were used to evaluate how well the data met the assumptions in the capture-recapture models (Pollock et al. 1985, Burnham et al. 1987).

Fecundity is defined as the mean number of female offspring produced per territorial female on a study area (Caughley 1977). Estimates of fecundity are based on the assumption that non-egg laying females were present on territories; an assumption that potentially underestimates fecundity. Annual fecundity was calculated on the current year's proportion of females that nested on the study area in the prior year. An analysis of variance (ANOVA) was performed on a year's reproductive output as the response variable using the general linear models (GLM) procedure in SAS (SAS Institute 1988) to test for significant time effects. Fecundity was calculated for each territorial female by dividing the nestlings produced by 2 (based on 1:1 sex ratio of fledglings, see below), and adjusting the standard error of the annual mean number of fledglings accordingly. Confidence limits (95%) for annual proportions of females breeding were calculated after Snedecor and Cochran (1969). Sex ratio of nestling goshawks was determined by counting the male and female nestlings in broods at the time of banding; only broods where the sex of all brood members was determined were included.

We attempted to investigate whether the Kaibab Plateau goshawk population was decreasing, stable, or increasing by calculating the finite rate of population change, lambda (λ). We estimated values of male and female juvenile survival necessary to obtain a value for λ of 1, or a stationary population, using the equation $S_o = (1-S)/b$, where S_o = necessary juvenile survival, S = adult survival, and b = fecundity (Noon and Biles 1990). Adult survival and fecundity values used in this equation were the survival and fecundity estimates for female and male non-juveniles on the Kaibab Plateau during the study period.

We determined the minimum number of territories and/or pairs of goshawks needed in a monitoring program to estimate nesting success, production of fledglings, and territory occupancy. We used bootstrap analyses (Efron and Tibshirani 1993) to assess possible bias and loss of precision in these estimates in reduced samples of territories and breeding pairs on the Kaibab Plateau in 1994-96. Actual data for each year represented the target population being estimated in bootstrap samples. Hypothetical samples were drawn with replacement from the observed data, and an estimate and associated standard error were computed for each sample. Samples (n =1000) were drawn for each sampling level (i.e., n =5, 10, 15 territories, etc.), and the distributions of estimates and standard errors displayed in box plots in which the observed (true) mean estimate and standard error were plotted. The potential bias and lack of precision associated with reduced samples of goshawk reproductive data is assessed in box plots by comparing the media hypothetical estimates with the "true" estimate, whether the box is symmetric about the "true" estimate, the width of the box (equivalent to 50% of the hypothetical estimates), and the size of potential large deviations from the "true" estimate as represented by the length of the wiskers (bounded by brackets) and presence of outlier estimates (asterisks).

RESULTS

Number and Occupancy of Territories

Numbers of territories included in the study increased each year as we annually expanded the study area (Table 1). In 1991, the majority (76%) of nests were located during searches in territories identified prior to 1991 (Reynolds et al. 1994). Subsequent to 1991, the majority of new territories were located in broadcasts and foot searches in areas between known territories and nest searches to expand the study area (see Figs. 1-6). By the end of the 1996 breeding season, about 95 percent of the National Forest lands, and about 30 percent of the GCNP (mostly in the northern and western portions) within the study area, had been searched for goshawk nests. A total of 107 territories were located and studied annually for a total of 478 territory-years (Figs. 1-7). All but three of the 107 territories contained pairs that laid eggs in one or more breeding season. The three exceptions were territories occupied two or more years by hawks that either built new nests or reconstructed old nests, but did not lay eggs.

From 1991 through 1993, the number of territories with active nests increased proportional to increases in total territories under study (Tables 1 and 2). In 1994 the number with active nests declined to 21, increased to 53 in 1995, and declined again to 46 in 1996 (Table 1). Annual increases in territories with "unknown status" reflected the difficulty of unambiguously determining the occupancy status (presence or absence) of goshawks on territories in years when they do not breed (Table 1). This ambiguity exists in spite of 8-10 person-days of foot and broadcasting searching for pairs in 800 m and 1,500 m radius circles around nests, respectively; territory occupancy can be demonstrated, but non-occupancy by the hawks cannot. Large numbers of territories with "unknown" status in 1994 reflects the number (n = 54) of territories in which active nests were not found and, because there were so many of these territories, we were unable to spend sufficient time in each to unambigously determine their occupancy status.

Nesting Sucess and Productivity

Table 2 displays the number and proportion of territories with active and failed nests and two measures of nesting success of traditional territories (excluding territories found in a current year). Because of their discovery in prior years, we were able to monitor nests in these territories from prior to egg laying, reducing bias due to variation in date of discovery in the current year. The annual proportion of territories with active nests followed the same annual pattern as with total territories monitored each year (Table 1); while slightly lower in all years, the highest proportions of territories with active nests occurred in 1991and 1992, followed by a decline in 1994, slight recovery in 1995, and another small decline in 1996. Percent of nests failing during the study was 31.3 percent in 1991, 18.4 percent in 1993, 27.8 percent in 1994, and 23.3 percent in 1995, and 25.6 in 1996. Annual estimates of nesting success were similar for the "traditional territory" and "Mayfield" visits for estimating nesting success; the two estimates differed by no more than 3 percentage points in any year, and neither was consistently higher or lower than the other (Table 2).

The 1991, 1992, and 1993 cohorts of territories had six, five, and four years of data, respectively (Table 3). In these cohorts, between 7-11 percent were active every year and between 4-28 percent were occupied for one year only. The majority (31 %) of territories were active for 5 years in the 1991 cohort, 3 years (41 %) in the 1992 cohort, and 2 years (50 %) in the 1993 cohort.

Brood size on the Kaibab Plateau ranged from 1 to 3 nestlings (median = 2 for all years); 28 percent of a total 224 successful broods (fledged at least 1 young) had one young, 50 percent had two young, and 22 percent had three young. The mean annual number of fledglings produced per active and successful nest on the Kaibab Plateau declined from the best years (highest proportion of pairs laying eggs) in 1991-1993 to lows in 1994-1996 (Table 4). Annual pattern in fledgling production (Table 4) reflected the annual pattern in the proportion of territories with active nests (Table 2) except that the number of fledgling produced did not recover to the same extent as did the proportion of pairs breeding in the two years after 1994.

Annual nesting success (proportion of nests fledging at least 1 young) on the Kaibab ranged between 72-86 percent for traditional territories (Table 2). Estimates of nesting success from traditional territories were similar to the Mayfield estimates -- both were within 1-3 percentage points each year (Table 2). Annual variations in nesting success followed the same patterns of variations in proportions of territories with active nests and annual production of young -- from highs in the early years (1991-1992) to lows in 1994-1995.

Of 273 nesting attempts in which eggs were laid on the Plateau, 46 (16.8 %) were known to have failed. Of the 46 failures, 16 (34.8 %) failed during the incubation period and 30 (65.2 %) failed during the nestling period. Of clutches that failed during incubation, four contained both fertile and infertile eggs, three contained only fertile eggs, and 12 contained only infertile eggs. Mean clutch size of these failed nests was 1.6 eggs (SD = 0.63, range = 1-3 eggs). Failures during the nestling period typically occured in the two weeks after hatching. We were unable to determine the causes of failure at these nests. Eggs buried in nests were recovered from 15 nests that fledged young; three nests contained fertile eggs, and 12 contained infertile eggs.

Fledgling Sex Ratio

We were able to determine the sex of all brood members in 125 broods. Combining years, sex ratio in broods was 126 females (54.3 %) to 106 males (45.7 %), not significantly different from a 1:1 sex ratio ($\chi^2 = 0.867$, df = 1, P = 0.352). There are no reports of unequal sex ratios of nestling goshawks in North America. However, in Wisconsin Cooper's hawks (*A. cooperii*) a sex ratio significantly skewed in favor of males (54%) over females (46%) (n = 372 broods) was reported (Rosenfield et al. 1996). A significantly skewed sex ratio in favor of males has also been reported in Harris's hawk (*Parabuteo unicinctus*) in New Mexico (Bednarz and Hayden 1991).

Distribution of Territories

Ripley's K function (Fig. 8) showed that centroids were spaced regularly at distances of 1,354-2,500 m, distributed randomly at inter-centroid distances of 2,500-5,000 m, and appeared aggregated at distances >8,500 m. We rejected (Cramer-von-Misses, P=0.00) the null hypothesis of a CSR process in overall distribution. Because clustering evident at large (>8,500 m) inter-centroid distances was assumed to reflect the shape of the study area and not true territory aggregation, we tested only the alternative spatial distribution of centroids between distances of 0-2,500 m. This latter range of distances was correctly modeled using the SSI process (Cramer-von-Mises, P=0.98; Fig. 9) indicating a regular distribution of centroids at these distances. The minimum distance between territory centers was 1,354 m.

Nearest-neighbor distances among the centroids of 103 (excluding 4 territories in the GCNP where intensive nest searches were not completed) with duplicate measures was 2.45 km (SD = 0.832 km). This is 0.6 km less than reported for nests in 59 territories on the Kaibab Plateau in 1991-1992 (Reynolds et al. 1994), and reflects the addition of 44 territories in an area only slightly larger than the area containing the 1991-92 sample of 59 territories. Nearest-neighbor spacing of the same 103 centroids above, without duplicate measures, was 3.88 km (SD = 0.322 km).

We estimated the potential total number of nesting pairs of goshawks on the Kaibab study area by calculating an exclusive circular area occupied by an "average" pair of goshawks using one-half of the mean nearest-neighbor distances without duplicate measures (3.88 km) as a radius and dividing the study area (173,168 ha) by the exclusive area (1,182 ha). The estimated total breeding population on the study area is about 146 pairs. The 107 territories identified during the study therefore represent about 73 percent of the potential nesting population on the Kaibab Plateau study area.

Movements Among and Spacing of Alternate Nests

Territorial pairs of goshawks often move from year-to-year to alternate nests within their territories (Reynolds and Wight 1978, Reynolds et al. 1994, Detrich and Woodbridge 1994). On the Kaibab Plateau, Reynolds et al. (1994) showed that colored-marked goshawks moved up to

635 m to nest in alternate nests. Of the 104 Kaibab territories in which eggs were laid, 59 contained alternate nests used during the study: 43 (41%) contained two alternate nests, 12 (12%) contained three alternate nests, and 4 (4%) contained four alternate nests. Of course, the more years territories are studied the greater the probability of discovery of additional alternate nests. The mean distance among alternate nests within territories was 489 m (SD = 541, min = 21 m, max = 3,410 m, median = 285 m, n = 103 territories). The frequency distribution of inter-alternate nest distances was strongly skewed to the right; 89.3 percent of alternate nests were within 900 m, and 95 within 1400 m, of one another (Fig. 10). On the Kaibab Plateau, the proportion of pairs that moved annually to alternate nests ranged between 52-73 percent ($\bar{x}$ = 60.4 %, SD = 8.53) (Table 5). On average, 20.3 percent of annual movements were to alternates used earlier in the study.

Natal and Breeding Dispersal

Natal dispersal is movement from a natal site to the site of first breeding (Greenwood and Harvey 1982). Of 256 goshawks marked as nestlings on the Kaibab Plateau, only 6 (3 males and 3 females) were subsequently recaptured as breeding adults on the study area (Table 6). Males were 3-5 years-old ($\bar{x}$ = 4.0 yrs-old) when first recaptured as breeders and had dispersed 10.3-23.0 km ($\bar{x}$ = 15.9 km, SD = 6.48 km), a distance equivalent to moving four territories from the natal site. Females were 2-4 years-old ($\bar{x}$ = 2.7 yrs-old) when first recaptured as breeders and had dispersed 15.0-32.0 km ($\bar{x}$ = 21.5 km, SD = 9.18 km), a distance equivalent to five territories from the natal site. Because the minimum distance to forest habitats from the Kaibab Plateau was 16 km, any juvenile dispersal to breeding sites off the Plateau would greatly increase the dispersal distance. No natal dispersal off the Plateau was detected; however, the recovery of a goshawk banded as a fledgling on the Plateau at 306 km suggests that long-distance natal dispersal could occur.

Breeding dispersal is movement between subsequent breeding territories (Greenwood and

Harvey 1982). Seven instances of breeding dispersal (2 males, 5 females) were recorded on the Kaibab Plateau during the study (Table 7). Mean male breeding dispersal distance was 2.8 km (SD = 1.06 km), a distance equivalent to moving to an adjacent territory, and 5.2 km (SD = 2.66 km) for females, a distance of about two territories from their first breeding territory. None of the dispersing breeders that changed territories moved more than once. All cases of breeding dispersal occurred between 1991-1993, the better breeding years of the study. Two of the dispersants were 2-year-old females, and the remainder were ≥ 3-year-old adults. Three of the dispersing hawks were recaptured on their new territories the year after the dispersal, while four others were recaptured 3-5 years after they were last seen on their original territory. Among the latter, it was possible that they established themselves on new territories in the year subsequent to their move but were not detected until later years.

Fidelity to Mate and Territory

Both male and female goshawks on the Kaibab Plateau showed a high degree of fidelity to their territories and mates (Table 8). Tenure on territories on the Plateau by females and males ranged from 1-6 years. Mean number of years goshawks in the 1991 cohort (n = 36 territories, 6 years of study) remained on territories was 1.42 years for males and 1.88 years for females. For the 1992 cohort of territories (n = 27 territories, 5 yrs of study), males remained on territories for a mean of 1.57 years and 1.77 years for females. Hawks in cohorts beyond 1992 were excluded because there were insufficient opportunities to show fidelity.

Overall, there was no significant difference in fidelity to territories in male and female goshawks on the Kaibab ($\chi^2 = 6.76$, df = 1, P <0.05, Binomial Proportion test). Breeding males remained faithful to their territories in 91.3 percent of cases, while females remained faithful in 77.8 percent of cases. In 50 known opportunities to change territories, seven adults (2 males, 5 females) changed territories, and none of these retained the same mate. We detected only one case of divorce, although we suspect two additional cases but were not certain of the status of mates. Overall, there was no difference in mate retention between the sexes ($\chi^2 = 7.49$, df = 1, P <<0.05, Binomial Proportion test).

Turnover on Territories

On the Kaibab Plateau the annual turnover rate varied from 0-40 percent for males and from 0-50 percent for females (Table 9). For both sexes, the year with fewest turnovers was 1994 -- the year with the lowest proportion of pairs laying eggs. The year of highest turnover for males was 1992 and 1995 for females. That no turnovers were detected for either sex in 1994 was probably related to the fact that so few pairs bred in 1994; also in 1994, recapture probabilities were low and there were few opportunities for detecting turnovers. With the exception of the high rate in 1992, annual turnover of males was relatively constant at about 20 percent; in contrast, female turnover rates lacked any annual consistency. The high turnover rate for females in 1995 may have been the result of increased mortality during the poor breeding year of 1994; there were no female breeding dispersals detected between in 1994 and 1995. Overall turnover rates for males and females during the 6-year study was 25 percent and 16 percent, respectively (Table 10).

Population Estimation

Sample Size and Goodness-of-Fit

During 1991-1996 we banded 449 goshawks on the study area, including 86 males and 87 females that were ≥ 3-years-old, 8 males and 12 females that were 1- or 2- years-old, and 256 nestlings (Table 11). Because only six of the banded nestlings were recaptured on the study area in subsequent years, we were unable to conduct goodness-of-fit tests and to estimate survival and recapture rates for the juvenile age class (<1-year-old). In addition, only 8 male and 12 female 1- or 2-year-old hawks were captured, too few to estimate survival rates for these age classes, we combined the 1- and 2-year-old hawks with the ≥ 3-year-old into a "non-juvenile" age class and defined the combined age class as hawks ≥ 1-year-old. Total sample of ≥ 1-year-old goshawks included in the capture-recapture analysis was 193 (94 males, 99 females). Number of times these hawks were captured (or resighted) and released (R_i) is presented in the capture-recapture *M*-array (Table 12). Annual recapture and resighting rates, as defined by Burnham et al. (1987), were 11-75 percent for male and female hawks ≥ 1-year-old (Table 12). The annual percentage of goshawks detected that were marked in previous years increased from 36 percent in 1992 to a mean of 49 percent (SD = 12.9) per year in 1993-1996 (Fig. 12).

Goodness-of-fit tests in program RELEASE (Burnham et al. 1987) showed that there were no differences in survival or recapture probabilities of ≥ 1-year-old male and female goshawks (Table 13). Test 3 indicated that goshawks within cohorts had similar future survival probabilities; Test 2 indicated that all marked hawks were equally trapable. Thus, there was no lack of fit to assumptions of Cormack-Seber-Jolly open population models.

Model Selection

Of the 64 models examined, the five most parsimonious models (those with the lowest AIC values) all had some time variation, and two had sex and time variation, associated with recapture probabilities (Table 14). Survival rates varied with sex in all except in one of the five best models. Three of the models had time effects on survival. The model with the lowest AIC value had seven parameters (2 sex, and 5 time parameters). Survival was a function of sex in this model ({Phi_s, P_t}) and was constant over years (Fig. 13). The model with the second lowest AIC value ({Phi_{s+T}, P_t}) had eight parameters and showed a sex and linear time trend increasing over years (Fig. 14). The top 4 models were nested, allowing likelihood ratio tests (LRT) for significance of differences among models. The LRTs showed no significant difference in model fit (differences in deviance) between any of the top 4 models. In the second and third models, survival varied over time, while there was no time variation in the first and fourth models.

Because the fit of these 4 models is not significantly different (P values, Table 14), there is no annual variation in survival, evidenced also by the wide confidence intervals in Figs. 14 and 15. Thus, although there may be some evidence for variation in survival over time, we were unable to detect it.

The constant annual survival estimates from the best model for the non-juvenile age class was 0.688 (SE = 0.0618) for males and 0.866 (SE = 0.0514) for females (Fig. 13). The linear time trend in survival rates of the second best-fitting model ranged from 0.540 (SE = 0.127) in the first year to 0.943 (SE = 0.118) in the last year for males, and from 0.825 (SE = 0.077) in the first year to 0.985 (SE = 0.036) in the last year for females (Fig. 14). All models with sex effects on survival had lower survival rates for male than females. The model with the fourth lowest AIC value (Phi_{s+t}, P_t) had 10 parameters and a no-sex effect survival estimate of 0.817 (SE = 0.048, both males and females) (Fig. 15).

The best five models had similar patterns of variable time effects on recapture probabilities. In all of these models recapture probabilities ranged from highs of 0.7 in 1992 to lows of 0.2 in 1994, followed by increases to 0.35 in 1996. Time effects on recapture probabilities correspond to the variable proportions of goshawk pairs laying eggs over years -- for the most part only nesting goshawks were captured or resighted.

Fecundity

Goshawks that do not lay eggs in a given year spend little time after the courtship period within the nest area. Consequently, it is often difficult to determine whether non-laying goshawks are occupying their territory. However, in most territories in years when goshawks do not lay eggs (Table 1), some evidence (observations of the hawks, feces, molted feathers, prey remains, fresh nest contruction) of occupancy is obtained, provided visits to nest areas occur early in the nesting period and/or enough time is spent in the cores of territories searching for the hawks. Physical evidence, combined with the frequent recapture of banded hawks at nests on their territories following a year of non-breeding, indicates that most non-laying goshawks continue to occupy their territories on the Kaibab Plateau.

Numbers of 1- and 2-year-old females were too few to calculate separate estimates of fecundity for these age classes. Therefore, the 1- and 2-year-old females were pooled with the ≥ 3-year-old females in estimates of fecundity. Estimates of mean fecundity of non-juvenile females during the study was 0.44 (SE = 0.35) (Fig. 16). Fecundity on the Kaibab was high in 1992-1993 and low in 1994-1996. Among-year variation in fecundity appeared to result from annual variation in proportion of pairs breeding. Some variation, however, may reflect among-year differences in nest failure rates (Table 2).

Estimation of Population Trends

Lambda (λ), the annual rate of population change, is computed from the adult and juvenile (age-specific) survival rates and fecundity rates (Franklin et al. 1996). Because too few juvenile goshawks were recaptured subsequent to their banding as nestlings on the Kaibab Plateau, we were unable to determine the survival rates of the juvenile age class and, therefore, could not calculate λ for the Kaibab goshawk population. Estimates of male and female juvenile survival values necessary to obtain a value for λ of 1, or a stationary population, given female (0.866) and male (0.688) non-juvenile survival rates and fecundity (0.44) on the Kaibab Plateau during the study, were 0.352 for juvenile females and 1.031 for juvenile males. The estimate of the necessary survival values for both sexes of juveniles when the survival of non-juvenile males and females are averaged (0.777), was 0.652.

Estimation of Sample Size

Plots of bootstrap sampling of the numbers of goshawks produced per nest (Figure 17) shows that a minimum of about 40 nesting pairs are needed to accurately estimate both the mean and standard error of the mean number of young, although occassional extreme mean and standard error values were generated in samples of 40 or more pairs. Likewise, a minimum of about 40 territories are needed to accurately estimate the proportion of nests that successfully fledge at least one young, although again a few extreme outlers in both means and standard errors were generated in samples of 40 or more territories (Fig. 18). Minimum number of territories needed to accurately estimate the proportion of pairs laying eggs range between 80 to 100 (Fig. 19).

DISCUSSION

While the mean annual numbers of fledglings produced per active nest on the Kaibab Plateau were within the range of values reported in other studies of North American goshawks, they tended towards the lower end of reported values. For example, Lee (1981) reported a mean per active nest of 3.8 young in Utah, McGowan (1975) reported 2.5 young in Alaska, and Younk and Bechard (1994) reported annual means of 2.0-2.8 young per active nest in Nevada. Mean numbers of young produced per successful nest on the Kaibab Plateau were also within the range of reported values, but were again at the lower end of the range. Doyle and Smith (1994) reported a mean of 3.9 young per successful nest in Canada, Lee (1981) 3.6 young in Utah, and McGowan (1975) 2.3-3.0 young per successful nest in Alaska. Mean annual nesting success on the Kaibab Plateau (77.2 %, Mayfield method) was also within the range of values reported for other goshawk populations but were low compared to other populations. For example, Reynolds and Wight (1978) reported nesting success of 90 percent in Oregon and Younk and Bechard (1994) reported success ranging from 84-100 percent in Nevada.

Mean natal dispersal distance on the Kaibab Plateau was similar to the mean (20.0 km) for two females in the California Cascades (Detrich and Woodbridge 1994). Age of first breeding of the six hawks on the Kaibab suggest that males enter the breeding population at an older age than females. Delayed breeding in males is also suggested by the rare reports of nesting juvenile males compared to more common reports of nesting juvenile females (Reynolds and Wight 1978, McGowan 1975, Younk and Bechard 1994). The greater natal dispersal distances of females is similar to observations in other avian species of females dispersing farther than males (Greenwood and Harvey 1982). Mean breeding dispersal distances on the Kaibab Plateau (4.5 km, both sexes combined) were somewhat less than means for male ($\bar{x}$ =6.5 km, SD = 2.7 km, n = 3) and female ($\bar{x}$ = 9.8 km, SD = 2.7 km, n = 4) goshawks in California (Detrich and Woodbridge 1994). Breeding dispersal in other raptors is usually to nearby territories (Reynolds and Linkhart 1987, Newton and Wyllie 1992). Fidelity to territory among Kaibab goshawks was somewhat higher than for male (76.5 %) and female (71.4 %) goshawks in California (Detrich and Woodbridge 1994), and for the congeneric European sparrowhawk (*A. nisus*) (70-75%) (Newton and Wyllie 1992).

Survival rates varied with sex in all except one of the five best models and with time in three of the best models. Survival for adult males was lower than for females in all models that had sex effects on survival. A similar difference in survival probabilities between the sexes was also reported for goshawks in California (DeStefano et al. 1994). The best five models had variable time effects on recapture probabilities, reflecting the variable annual proportion of pairs breeding and opportunities for recapturing hawks.

We were unable to recapture a sufficient number of juvenile hawks on the Kaibab Plateau to estimate juvenile survival, and a radio-tracking study of dispersal and juvenile survival was discontinued due to insufficient funding in 1993. However, estimates of the necessary juvenile survival to obtain a $\lambda = 1$ (a stationary population), given the female and male non-juvenile survival rates and mean fecundity on the Kaibab Plateau, for juvenile females were is within the reported range of juvenile survival in other raptors (Forsman et al. 1996). Thus, both the adult female survival and estimates juvenile female survival rates seem reasonable. However, the high survival rate for juvenile males needed to maintain a stationary population is biologically impossible. As a result, we have little confidence in our estimate of adult male survival rates on the Kaibab Plateau. Our estimates of survival include the capture-recapture histories of nearly 200 adult goshawks over six years, yet there were small numbers of recaptures in some years, especially 1994. While the limited recaptures did not result in overall model rejection, the marginally-significant survival probabilities for male goshawks suggests the need for additional years of capture-recapture study.

Our capture-recapture estimate of adult male survival on the Kaibab may have been biased low by a higher emigration rates of male versus females from our study area. However, greater territory fidelity and a shorter (detected) breeding dispersal distances of males suggest that a higher emigration rates of males is not likely. It is also possible that lower male survival reflects their greater age (senescence) on entering the breeding population and the capture-recapture data set. Whether older hawks have lower survival probabilities is unknown. Finally, males may also have lower survival because they do most of the foraging during nesting and are as a consequence exposed to high rates of accidents, predation, and exhaustion.

In spite of low male survival, there is evidence that the goshawk population on the Kaibab is both saturated and relatively stable. Regular spacing of territories at relatively short nearest-neighbor distances (Reynolds and Wight 1978, Woodbridge and Detrich 1994), and the high annual rate of occupancy of territories by hawks, is suggestive of a saturated population. Low recruitment and the age of hawks when first recruited into the breeding population suggest that most territories are occupied and hawks must wait 2-5 years before territories become available. High fidelity of both adult sexes to mates and territories also suggests that other breeding areas on the Kaibab are occupied. If there is competition for territories, hawks that abandon a territory may not find an available territory and may give up their own. In spite of the above, not all territories were equal in numbers of years in which the territorial pair nested and numbers of young produced during the study.

Annual variation in the proportion of pairs laying eggs, nest success, productivity, fecundity, and recapture rates of goshawks on the Kaibab Plateau appeared to be related to annual variations in at least one main goshawk prey species, the red squirrel (*Tamiasciurus hudsonicus*). In 1991 and 1992 red squirrels increased in abundance. At the end of the 1992 breeding season, red squirrels were very abundant and had spread into ponderosa pine and pinyon-juniper forests at lower elevations. In early summer of 1992, the populations of the Abert's squirrel (*Sciurus aberti kaibabensis*) and the golden-manteled ground squirrel (*Spermophilius lateralis*) also appeared to be higher than in 1991. By late summer of 1993, observations indicated that at least red squirrels began to decline, and in spring and summer of 1994, observations of red squirrels in any of the forest types on the Kaibab Plateau were rare. After goshawk eggs hatched in 1994, the few female goshawks that laid eggs were seldom in their nest areas during our regular nest visits -- presumably to supplement the males foraging. In 1995 and 1996, red squirrel populations seemed to recover somewhat.

Fluctuations in numbers of nesting goshawks occur in other Northern American goshawk populations, notably in Alaska and Canada, where important goshawk prey such as snowshoe hare (*Lepus americanus*), red squirrel, and grouse (*Dendragopus* spp.), are subject to extreme population fluctations (McGowan 1975, Doyle and Smith 1994). Populations of tree squirrels and other prey species dependent on conifer seed can fluctuate similarily depending on fluctations in conifer cone crops, which exhibit simultaneous variation over large geographic areas (Garman 1951, Smith 1968, Smith 1970).

Monitoring: Procedures, Sample Sizes, and Effort

A likely objective of a goshawk monitoring program is to measure, with adequate reliability, changes in goshawk poppulation size and associated demographic variables such as survival, recruitment, and reproduction. Each of these demographic variables can be affected by hawk abundance, the quality and availability of their foods, rates of emigration and immigration, weather, habitat quality, and anthropogenic habitat modification. Because most avian monitoring programs are motivated by concerns for the effects of habitat changes on species, many monitoring programs also focus on the habitat of species. However, in most cases there is insufficient information on the specific demographic or habitat variables of interest, sample sizes required for accurate population estimates, sizes of sampling areas, timing of sampling, and sampling effort, to specify suitable monitoring designs and sampling protocols.

The following recommendations for monitoring goshawk populations are focused on a few demographic variables typically assessed in an avian monitoring program. The recommendations are based on our six year "pilot study" (1991-1996) of goshawks on the Kaibab Plateau on which other parts of this report are based. Recommendations on the timing of monitoring activities, the sample of required territories, and skills and number of field persons are specific to the the conditions on the Plateau -- the local density of goshawks, accessibility to their territories, and the local breeding season phenology. However, with adjustments for nesting phenology, nest density, terrain and road densities, the recommendations should have general applicability for other goshawk populations. We recommend procedures, sample sizes, and levels of effort required to estimate reproductive status of hawks on territories, production of young, nesting success, and proportion of territorial pairs that lay eggs.

Reproductive status of territories. -- Most pairs of goshawks appear to attempt to lay eggs every year and their pre-egg laying activities are typically associated with a nest structure. However, many pairs fail to lay eggs and non-laying hawks spend little additional time after failing to lay in their nest area. Therefore, estimating the occupancy status of territories in which eggs are not laid requires regular visits to nests in the period between three weeks prior to, and one week after, the egg laying. The more frequent the visits to known nest areas, the greater the probability of detecting occupancy. Three, half-day visits to known nest structures during this period are recommended. Evidence for occupancy should include two or more visual or auditory observations of hawks and/or at least three of the following: abundant feces, molted feathers, prey remains, and freshly reconstructed nests in nest areas. Thorough searches for evidence within 200 m radius of all nest structures should be conducted during this period (Reynolds 1982). Because non-occupancy of territories by goshawks is almost impossible to prove, occupancy rate may be a poor estimate of the status of a goshawk population.

Between 50 and 73 percent of territorial pairs move to alternate nests within their territories annually. Searching for pairs that may have moved often amounts to the largest investment of time in a goshawk monitoring program. If annual searches for pairs of hawks that have moved are not made, then a "decay" in a known sample of goshawks will occur, suggesting of a population decline when it may be stationary. On discovering that a pair of hawks are not using known alternate nests, we recommend some combination of foot and broadcast searching within a circular area of 1,500 m radius centered on the last-used nest tree. Searching within that radius should detect of 90-95 percent of alternate nests. Both nest-search procedures can be used through the breeding season. However, because broadcasting is least effective at eliciting responses from goshawks during the incubation and early nesting periods, foot searching is the most effective procedure during the first half of the breeding season. Foot search requires greater observer experience with goshawks and signs of their presence than does broadcast; for less skilled field crews broadcast is the preferred procedure. In the latter case, the standardized transect and broadcast station procedure should be used (Joy et al. 1994).

Nest productivity. -- Productivity can be measured by clutch size or numbers of nestlings. The most accurate estimate of productivity is a count of nestlings at or near the end of the nestling period. Accurate estimates of productivity typically require tree climbs to nests. To avoid disturbing adults during the disturbance-sensitive incubation and early nesting periods, and to minimize the possibility of forcing nestlings to prematurely jump from nests, climbs should be limited to the fourth week of the nestling period, when nestling are 25-30 days-old. Counts of hawks after fledging underestimate productivity due to the likelihood of miss-counting fledglings.

Nesting success. -- Either the monitoring of traditional nests or the Mayfield method gives accurate estimates of nesting success. However, in the first years of a monitoring program, when territorial pairs are still being added to the sample throughout a season, the Mayfield method is superior because it allows all nests to be included in an estimate of success. When the reproductive status of a large (> 35 territories) sample of territories can be monitored from egg laying, the traditional territory method is more easily implemented. Regular (weekly) visits to nests are recommended so that the timing and possible causes of losses can be determined.

Sample size. -- Bootstrap analyses suggested that about 35-40 territorial pairs of goshawks are needed for precise estimates of nest productivity and nesting success. However, estimates of the proportion of pairs laying eggs, a variable required for estimating fecundity, requires between 80 and 100 pairs. These large samples and the degree of difficulty of finding nests of goshawks are the main cost components of a goshawk monitoring program.

Density. -- Numbers of pairs of goshawks per unit area can be determined only in intensive, systematic searches of large forests areas. Nest searches must be repeated over years to avoid missing non-breeding pairs. Once an estimate of local nest spacing is determined, inter-nest distances help focus searches in "holes" where pairs have not been found. These distances, however, should serve only as guides. Years of repeated intensive searches result in a complete count of territories on an assessment area. A benefit of a complete count is the capability of associating gaps in the distribution of goshawk pairs with local habitat conditions. Using the spacing of goshawk nests on the Plateau as a basis, approximately 500 km^2 of forest habitat is needed to contain about 40 pairs of goshawks, and 1,000 km^2 is needed for 80 pairs of goshawks.

Survival. -- The capture-recapture method for estimating survival probabilities requires annually capturing or resighting of hawks at their nest areas. Our estimates of survival are based on six years of capturing/resighting (5 recapture occasions) efforts and included 94 adult males and 99 adult females. Our estimate of juvenile male survival (1.031) necessary to maintain $\lambda = 1$ is biologically unattainable, yet a number of attributes of the Kaibab goshawk population suggests that it is stable. This led us to suspect that the survival estimate for adult males was biased low and that additional years of capture/resighting are needed for more reliable estimates. Thus, for a monitoring program in which adult survival is to be estimated, we recommend a minimum of six recapture occasions (years) and the inclusion of at least 100 individuals of each sex.

Effort. -- The combined activities associated with initial visits to territories to determine reproductive status of pairs, searches for pairs that may have moved to alternate nests, weekly visits to active nests, and assessments of productivity required about one field person per 8 goshawk territories. Thus, 5 persons are needed to monitor 40 territories and between 10-13 persons to monitor 80 to 100 territories. Additional persons are required to conduct the initial searches for pairs during the early years to increase the sample of pairs. If capture-recapture estimates of survival are required, than one to two 2-person trapping crews are needed for 40 territories, and three trapping crews are needed for 80 to 100 territories.

ACKNOWLEDGMENTS

This research was funded by the USDA Forest Service, Southwestern Regional Office, the Kaibab National Forest, the North Kaibab Ranger District, the Rocky Mountain Forest and Range Experiment Station, and a Heritage Program grant from the Arizona Game and Fish Department. For help with nest searching, capturing and measuring goshawks, climbing nest trees, radio-tracking goshawks, censusing prey populations, and denting trucks, we thank S. Bedard (5 yrs), C. Boam, C. Erickson, M. Gavin, D. Laing, D. Leslie, J. Seyfried, J. Wiens (4 yrs); R. Brogel, J. Burns, B. Hunt (3 yrs); P. Clark, G. Dilworth, T. Gamberg, L. Hunt, D. Rubinoff, S. Salafsky (2 yrs); A. Alfonso, R. Albers, G. Bayluss, K. Boden, R. Brunotte, J. Dudley, S. Dudley, I. Gilmore, K. Kalin, T. Kelley, J. Koloszar, T. Rice, L. Schultz, M. Sherman, J. Sneva, S. Spidle, D. Strait, J. Whittier, and D. Worthington (1 yr). S. Bedard, R. Brogel, M. Gavin, S. Salafsky helped with data entry and analysis. E. Forsman and J. Reid provided input on running programs RELEASE and SURGE and interpretating results. R. King advised on subsampling and J. Williams performed the bootstrap analysis of the reproductive data. V. Thomas helped develop graphics with ARC/INFO, R. Reich provided guidance with S-PLUS programming, and D. Dean helped with Geographic Information Systems theory.

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Table 1. Number of territories under study, active, occupied, and unknown status of northern goshawks on the Kaibab Plateau, Arizona, 1991-1996.

Territories	Year					
	1991	1992	1993	1994	1995	1996
Total	37	64	82	88	100	107
Active	36	59	67	21	53	46
Occupied	1	2	6	13	20	23
Status unknown	0	3	9	54	27	38

100

Table 2. Nesting success of northern goshawks on the Kaibab Plateau, Arizona, 1991-1996. Number of traditional territories (territories included in study from previous years) studied each year, number and percent with active nests, number and percent with failed nests, and two estimates of nest success. Mayfield (1975) estimate of nesting success included for comparison.

Territories	Year				
	1992	1993	1994	1995	1996
Total from previous year	37	64	82	88	100
Number with active nests	32	49	18	43	39
Percent with active nests	86.5	76.6	22.0	48.9	39.0
Number with failed nests	10	9	5	10	10
% failed nests	31.3	18.4	27.8	23.3	25.6
% success, traditional	81	86	72	74	74
% success, Mayfield	79	83	75	76	73
SE, Mayfield	0.002	0.001	0.003	0.001	0.002

Table 3. Proportion of six cohorts (1991-1996) of 104 northern goshawk territories that contained active nests for 1, 2, 3, 4, 5, and 6 years, not necessarily consecutive, on the Kaibab Plateau, Arizona, 1991-1996. Cohorts of territories are territories found in a given year. Number of territories are in parentheses.

Year	Territories in cohort	Years					
		1	2	3	4	5	6
1991	36	0.06 (2)	0.14 (5)	0.28 (10)	0.16 (5)	0.31 (11)	0.08 (3)
1992	27	0.04 (1)	0.33 (9)	0.41 (11)	0.15 (4)	0.07 (2)	
1993	18	0.28 (5)	0.50 (9)	0.11(2)	0.11 (2)		
1994	5	0.20 (1)	0.80 (4)				
1995	11	0.73 (8)	0.27 (3)				
1996	7	1.00 (7)					

Table 4. Number of active (egg laid) and successful (fledged at least 1 young) nests, and mean number and standard deviation (SD) of fledglings per active and successful nests of northern goshawks on the Kaibab Plateau, Arizona, 1991-1996.

	Year					
	1991	1992	1993	1994	1995	1996
Active nests[1]	36	59	64	21	49	44
Fledglings/active nest	2.0	1.8	1.7	1.2	1.3	1.3
SD	0.79	1.05	1.00	0.93	0.92	0.90
Successful nests[1]	34	49	54	15	39	33
Fledglings/successful nest	2.1	2.2	2.0	1.7	1.6	1.7
SD	0.64	0.72	0.74	0.62	0.71	0.59

[1] Number of nests where exact number of fledglings was determined.

Table 5. Proportion of northern goshawk pairs annually moving to alternate nests within their territories on the Kaibab Plateau, Arizona, 1991-1996. Number of cases are in parentheses.

Movement	Year					
	1992	1993	1994	1995	1996	Total
None	0.47 (15)	0.38 (18)	0.39 (7)	0.48 (19)	0.27 (10)	0.39 (69)
To new alternate	0.53 (17)	0.50 (24)	0.39 (7)	0.38 (15)	0.41 (15)	0.45 (78)
To prior alternate		0.12 (6)	0.22 (4)	0.15 (6)	0.32 (12)	0.16 (28)
% Total moving	53	63	61	52	73	61

Table 6. Natal dispersal of northern goshawks on the Kaibab Plateau, Arizona, 1991-1996. Sex and year nestling was banded, year and age when first found breeding, and dispersal distances.

Sex	Year banded as nestling	Year of 1st breeding	Age	Dispersal distance (km)
Male	1991	1996	5-yrs-old	14.4
Male	1992	1995	3-yrs-old	23.0
Male	1992	1996	4-yrs-old	10.3
Female	1991	1993	2-yrs-old	17.5
Female	1991	1993	2-yrs-old	32.0
Female	1991	1995	4-yrs-old	15.0

Table 7. Breeding dispersal in northern goshawks on the Kaibab Plateau, Arizona, 1991-1996. Sex, year, and age when last captured on original territory, year recaptured, and dispersal distances.

Sex	Yr last captured original territory	Age at last capture	Yr captured on new territory	Dispersal distance (km)
male	1991	≥3-yr-old	1992	3.5
male	1992	≥3-yr-old	1996	2.0
female	1991	2-yr-old	1992	2.4
female	1991	≥3-yr-old	1992	8.6
female	1991	≥3-yr-old	1996	3.2
female	1992	2-yr-old	1996	7.3
female	1993	≥3-yr-old	1996	4.5

Table 8. Territory and mate fidelity in northern goshawks nesting on the Kaibab Plateau, Arizona, 1991-1996. For "different mate" categories, only pairs of hawks known to be alive in subsequent years are included. Numbers in parentheses are cases in categories.

Pattern	Percent of males	Percent of females	Percent overall
Same territory			
same mate	91.7 (22)	78.6 (22)	84.6 (44)
different mate	-	3.6 (1)	1.9 (1)
Different territory			
same mate			
different mate	4.2 (1)	-	1.9 (1)
unknown[1]	4.2 (1)	17.9 (5)	11.5 (6)
Total cases	24	28	52

[1]Includes males and females who changed territories and paired with a different mates, but status of original mate could not be determined (1 male, 2 females), and females who changed territories but identity of original or successive male was unknown (3 females).

Table 9. Annual turnover of male and female northern goshawks on the Kaibab Plateau, Arizona, 1991-1996.

	1992		1993		1994		1995		1996	
	M	F	M	F	M	F	M	F	M	F
Turnovers	4	3	3	2	0	0	1	3	1	2
Opportunities[1]	10	19	12	22	4	5	5	6	5	11
% turnover	40	16	23	9	0	0	20	50	20	18

[1]Opportunities = number of breeding seasons (subsequent to the year when an individual breeding hawk was first captured and banded on a territory) in which either an original or new breeding hawk was captured (identified) on that territory.

Table 10. Total turnover of nesting northern goshawks on territories on the Kaibab Plateau, Arizona, 1991-1996.

	Male	Female	Overall
Turnovers	9	10	19
Opportunities[1]	36	63	99
Percent turnover	25.0	16.0	19.2

[1]Opportunities = number of breeding seasons (subsequent to the year when an individual breeding hawk was first captured and banded on a territory) in which either the original or new breeding hawk was captured (identified) on that territory.

Table 11. Number of northern goshawks captured and banded by year, sex, and age class on the Kaibab Plateau, 1991-1996.

Year	Adult (≥ 3 yrs) females	Adult (≥ 3 yrs) males	1-2-yr-old females	1-2-yr-old males	Juveniles
1991	26	21	2	1	45
1992	15	20	6	2	32
1993	11	13	3	3	66
1994	5	5	1	2	19
1995	21	18	0	0	52
1996	9	9	0	0	42
Totals	87	86	12	8	256

Table 12. Capture-recapture data in *M*-array format for female and male northern goshawks initially captured as ≥1-year-old adults on the Kaibab Plateau, Arizona, 1991-1996. R_i is the number of hawks marked and released on the ith occasion, M_{ij} the number of hawks marked and released on occasion *i* which were recaptured (or resighted) on occasion *j*, and r_i the total number of hawks marked and released on occasion *i* which were later recaptured ($= \sum M_{ij}$).

			M_{ij} for $j =$					
Age class	*i*	R_i	2	3	4	5	6	r_i
Non-juvenile (≥1yrs) male	1	19	7	2	0	1	0	10
	2	19		8	1	1	1	11
	3	28			5	2	3	10
	4	14				4	0	4
	5	27					4	4
Non-juvenile (≥1yrs) female	1	28	18	11	3	0	0	21
	2	39		20	0	3	4	27
	3	37			5	4	5	14
	4	11				3	1	4
	5	30					9	9

Table 13. Goodness-of-fit tests from program RELEASE (Burnham et al. 1987) for capture-recapture data from non-juvenile (≥ 1-yr-old) male and female northern goshawks on the Kaibab Plateau, Arizona, 1991-1996.

Sex	TEST 2	TEST 3	TEST 2+3[1]		
	P	P	x^2	df	P
Male	0.5954	0.2452	7.33	9	0.6029
Female	0.8371	0.9176	1.97	10	0.9966

[1]TEST 2 tests for statistical independence among sex cohorts and individuals. TEST 3 tests whether previously captured and released hawks have the same future fates as newly released hawks.

Table 14. Capture-recapture models for estimating survival of northern goshawks on the Kaibab Plateau, Arizona, 1991-1996. Models that best fit the data are indicated by lowest AIC values (Akaike's Information Criterian, Akaike 1973). Models are shown in order of increasing Akaike's Information Criterion (AIC) values. K is the number of estimable parameters for each model.

				LRT		
Model[1]	Deviance	K	AIC	χ^2	df	P
$\{Phi_s, P_t\}$	490.126	7	504.13			
$\{Phi_{s+T}, P_t\}$	488.192	8	504.19	1.93	1	0.165
$\{Phi_{s+T}, P_{s+t}\}$	487.558	9	505.56	0.64	1	0.424
$\{Phi, P_{s+t}\}$	491.695	7	505.69	4.14	2	0.126
$\{Phi_{s+t}, P_t\}$	485.745	10	505.75			

[1]Subscripts associated with Phi (survival) and P (recapture probability) indicate these parameters have a linear time trend (T), a variable time effect (t), a sex effect (s), or some additive effect. Models of Phi and P without subscripts indicate no time or sex effects on survival or recapture rates.

Figure 1. Locations of nests in which eggs were laid by northern goshawks on the Kaibab Plateau, Arizona in 1991.

Figure 2. Locations of nests in which eggs were laid by northern goshawks on the Kaibab Plateau, Arizona in 1992.

Figure 3. Locations of nests in which eggs were laid by northern goshawks on the Kaibab Plateau, Arizona in 1993.

Figure 4. Locations of nests in which eggs were laid by northern goshawks on the Kaibab Plateau, Arizona in 1994.

Figure 5. Locations of nests in which eggs were laid by northern goshawks on the Kaibab Plateau, Arizona in 1995.

Figure 6. Locations of nests in which eggs were laid by northern goshawks on the Kaibab Plateau, Arizona in 1996.

Figure 7. Locations of centroids for alternate nests within of 107 northern goshawk territories on the Kaibab Plateau, Arizona, 1991-1996.

Figure 8. K function showing the actual distribution (solid line) of northern goshawk territory centroids (1991-1996) 0-15,000 m compared with the distribution of a hypothetical goshawk population (dashed line) modeled under complete spatial randomness (CSR). Regular spacing of centroids is indicated at inter-territory distances where the actual distribution falls below the confidence envelopes for CSR.

Figure 9. K function showing the actual distribution (solid line) of northern goshawk territory centroids (1991-1996) at inter-centroid distances of 0-5000 m compared with the distribution of a hypothetical goshawk population modeled with a simple sequential inhibition (SSI) process (dashed line). The model correctly captures the regular spacing of centroids between 2500 m and 1354 m. No territory centroids occur within 0-1354 m of other centroids in the actual population. Variegated lines represent 95% confidence limits around the SSI population.

Figure 10. Frequency distribution of inter-alternate nest distances within goshawk territories.

Figure 11. Proportion of non-juvenile ($\geq$ 1-yr-old) northern goshawks detected on the Kaibab Plateau banded in previous years, 1991-1996.

Figure 12. Estimates of annual survival for non-juvenile ($\geq$ 1-yr-old) northern goshawks on the Kaibab Plateau, Arizona, 1991-1996. Horizontal lines represent constant survival estimates for males (broken line, $Phi_s = 0.688$, SE = 0.0618) and females (solid line, $Phi_s = 0.866$, SE = 0.0514) from the best model (Phi_s, P_t).

Figure 13. Estimates of annual survival for non-juvenile (≥ 1-yr-old) male (top) and female (bottom) northern goshawks on the Kaibab Plateau, Arizona, 1991-1996. Line in graph represents the nearly linear time trend in survival estimates from the second-best model (Phi_{s+T}, P_t).

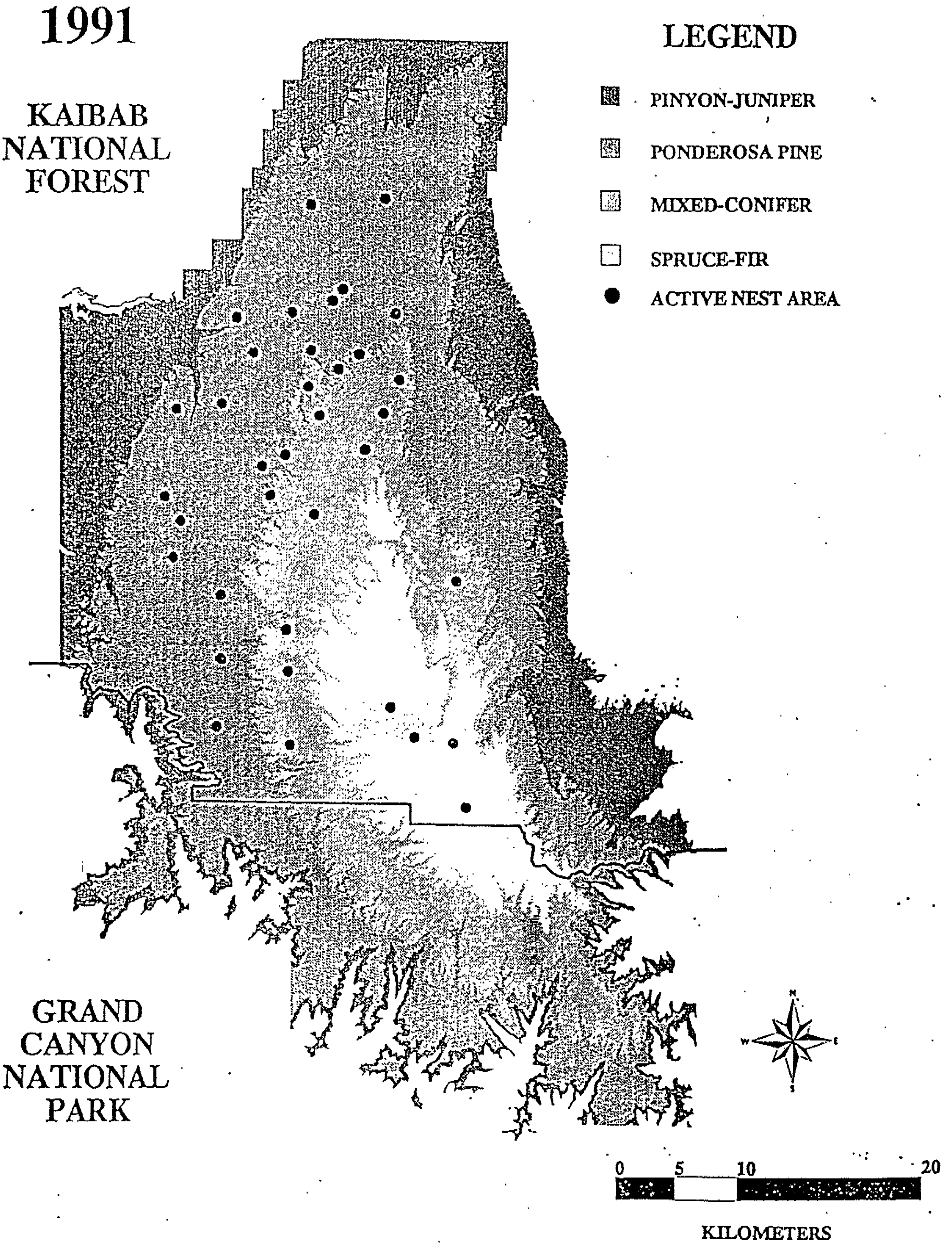
Figure 14. Estimates of annual survival for non-juvenile (≥ 1-yr-old) male (top) and female (bottom) northern goshawks on the Kaibab Plateau, Arizona, 1991-1996. Line in graph represents the annual survival estimates from a variable time model (Phi_{s+t}, P_t).

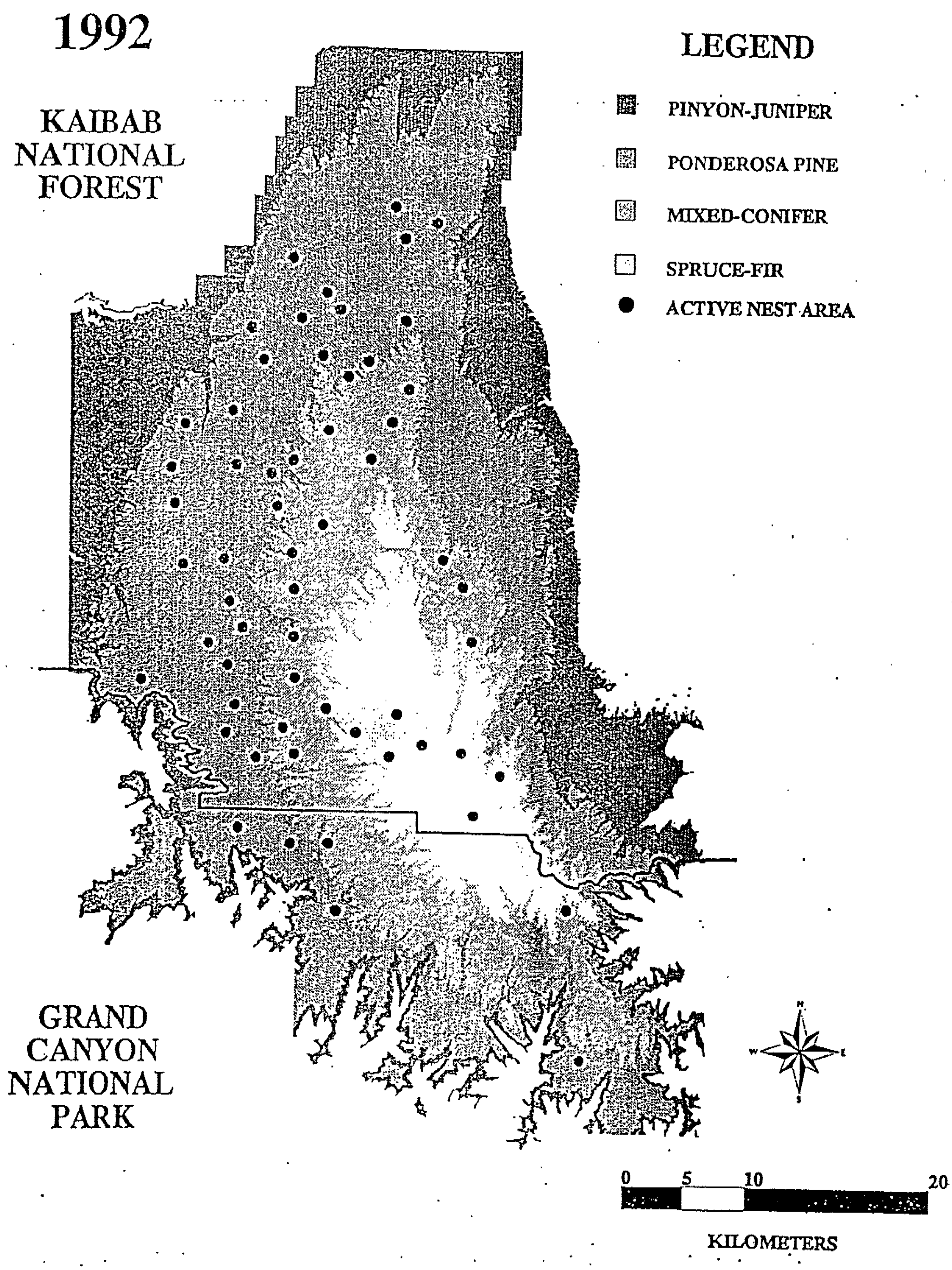
Figure 15. Annual fecundity (with standard errors) and proportions of female northern goshawks nesting on the Kaibab Plateau, Arizona, 1991-1996.

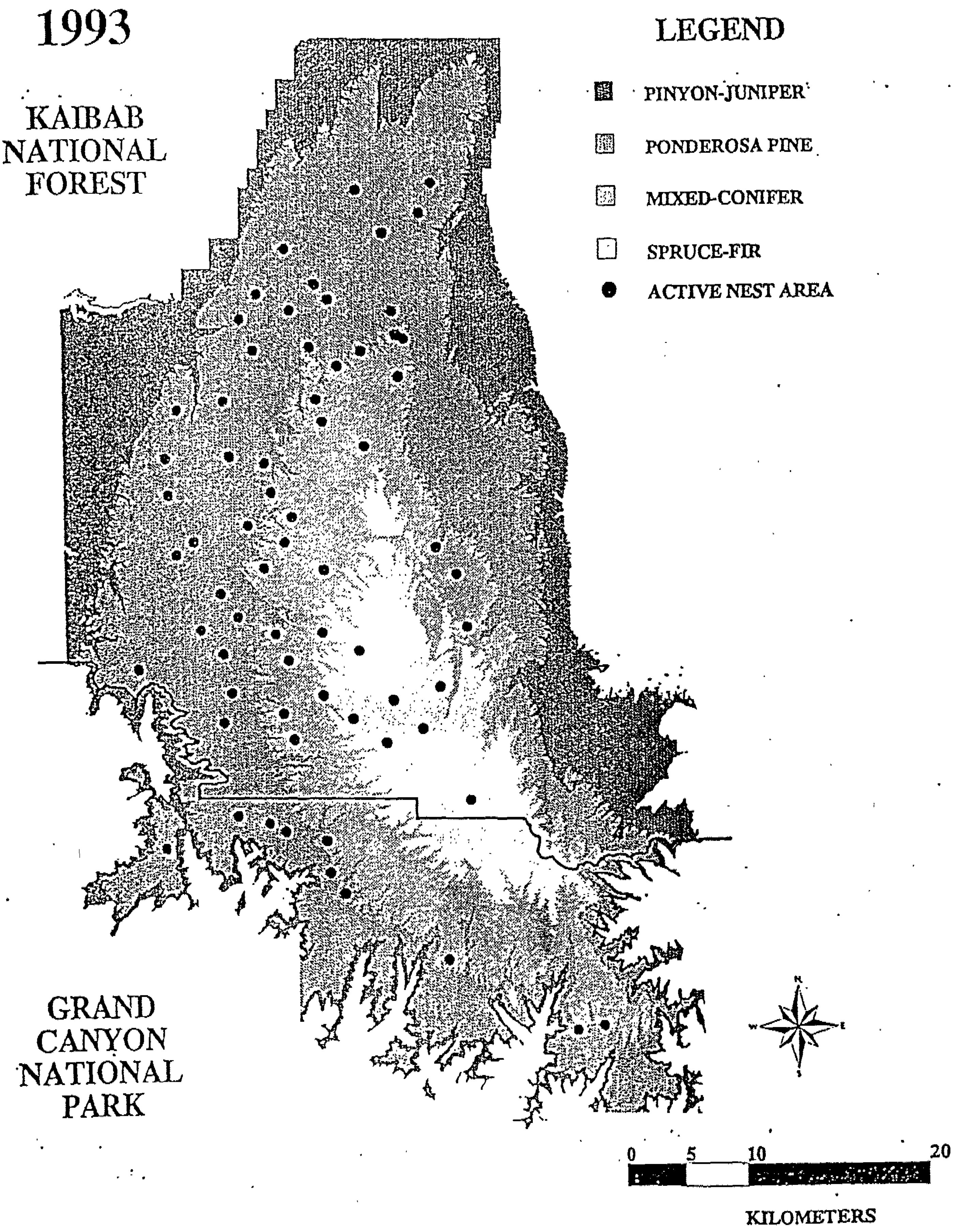
Figure 16. Box plots of bootstrap samples of the target population (number of young fledged/nest/year from goshawk nests) on the Kaibab Plateau in 1994, 1995, and 1996. Total active (eggs laid) nests in target populations (solid verticle line) was 22 in 1994, 47 in 1995, and 44 in 1996. Parameters of the target populations (solid horizontal lines) were mean = 1.19 and SE = 0.203 in 1994, mean = 1.30 and SE = 0.140 in 1995, and mean = 1.23 and SE = 0.130 in 1996.

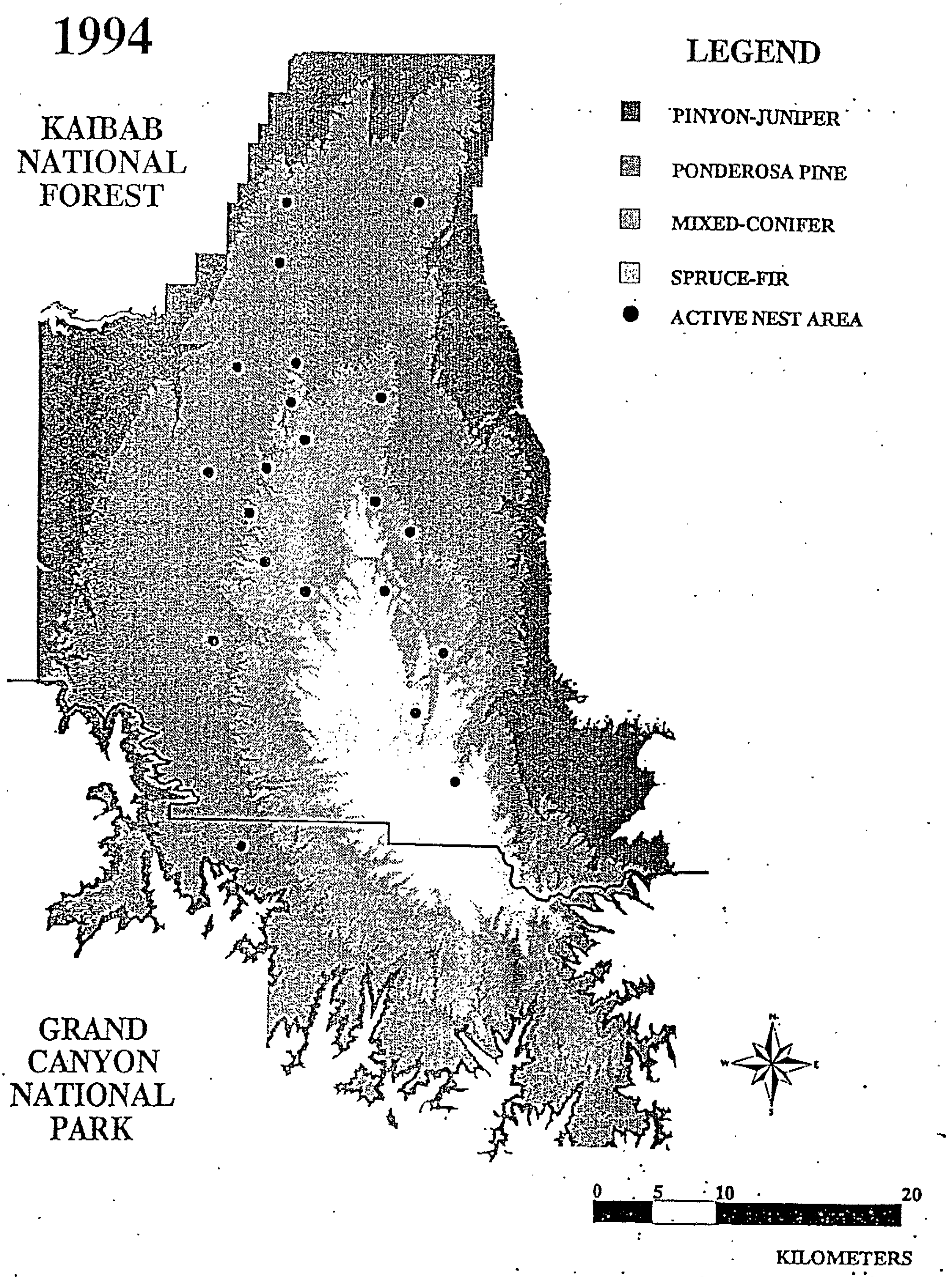
Figure 17. Box plots of bootstrap samples of the target population (proportion of goshawk nests producing at least 1 fledgling/year) on the Kaibab Plateau in 1994, 1995, and 1996. Total active (eggs laid) nests in target populations (solid verticle line) was 22 in 1994, 47 in 1995, and 44 in 1996. Parameters of the target populations (solid horizontal lines) were mean = 0.17 and SE = 0.100 in 1994, mean = 0.77 and SE = 0.006 in 1995, and mean = 0.75 and SE = 0.066 in 1996.

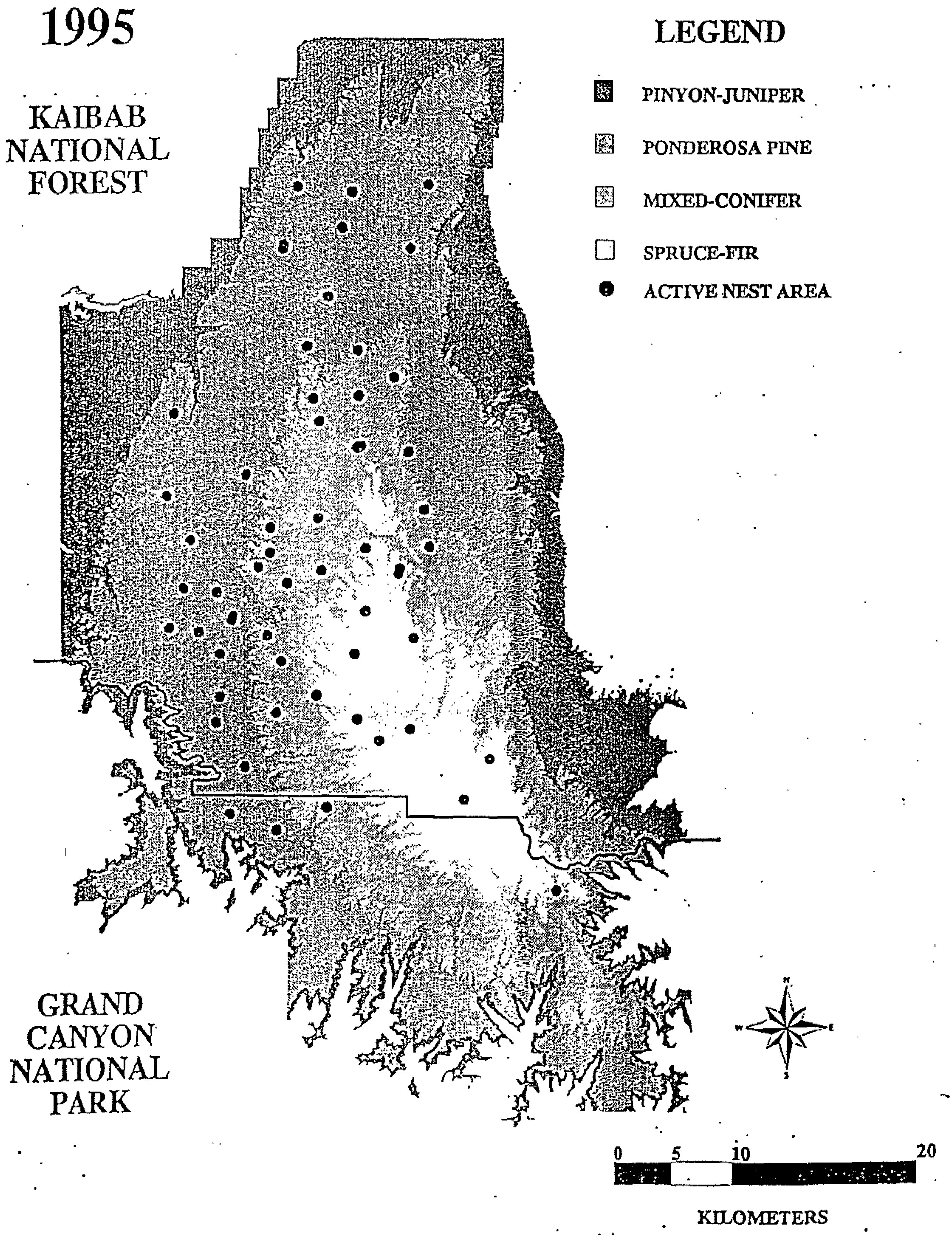
Figure 18. Box plots of bootstrap samples of the target population (proportion of goshawk territories with active nest/year) on the Kaibab Plateau in 1994, 1995, and 1996. Total territories in target populations (solid verticle line) was 88 in 1994, 100 in 1995, and 107 in 1996. Parameters of the target populations (solid horizontal lines) were mean = 0.22 and SE = 0.046 in 1994, mean = 0.50 and SE = 0.054 in 1995, and mean = 0.39 and SE = 0.049 in 1996.

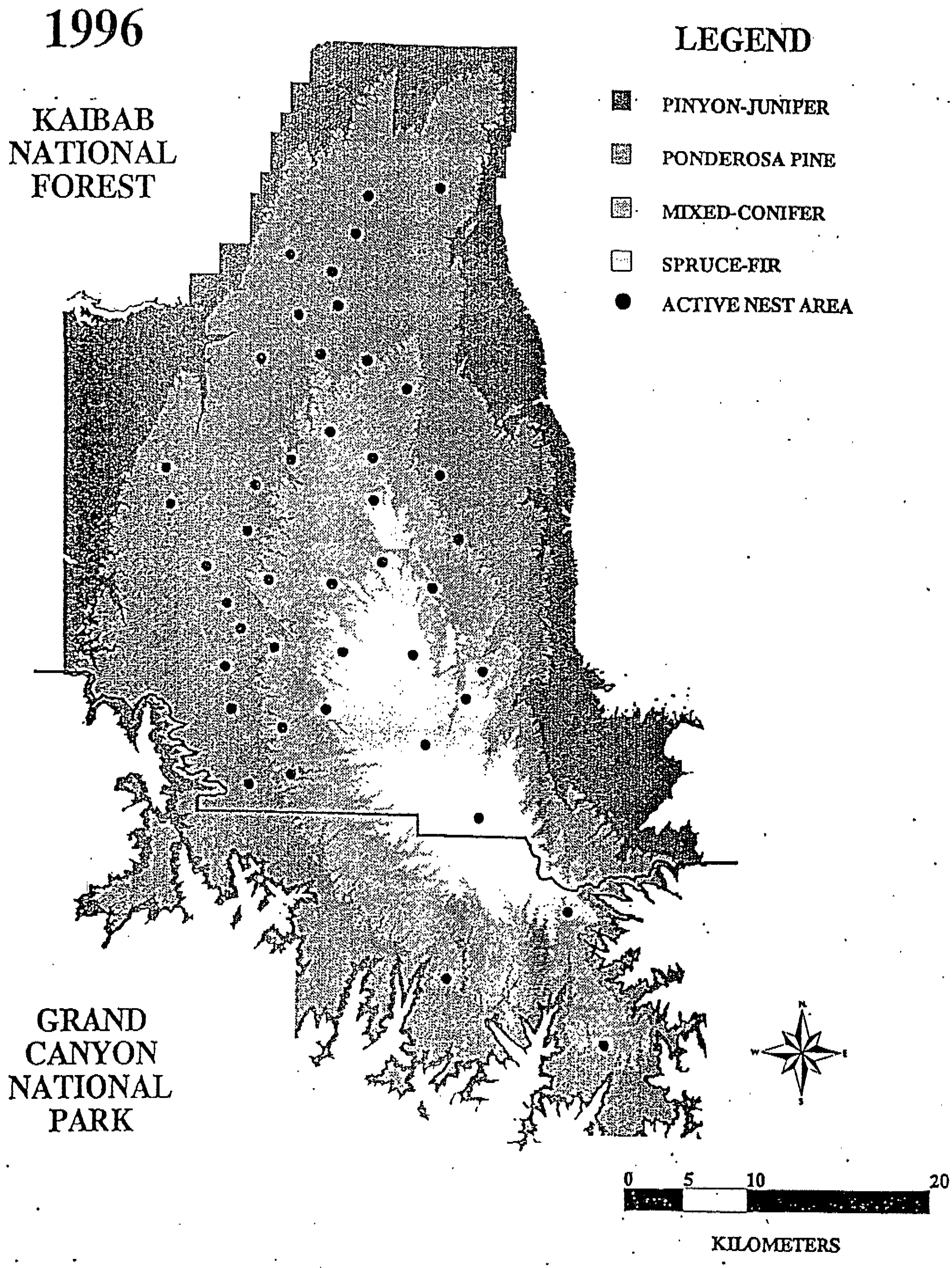

1991
KAIBAB
NATIONAL
FOREST
LEGEND
PINYON-JUNIPER
PONDEROSA PINE
MIXED-CONIFER
SPRUCE-FIR
ACTIVE NEST AREA
GRAND
CANYON
NATIONAL
PARK
N
W
E
S
0
5
10
20
KILOMETERS

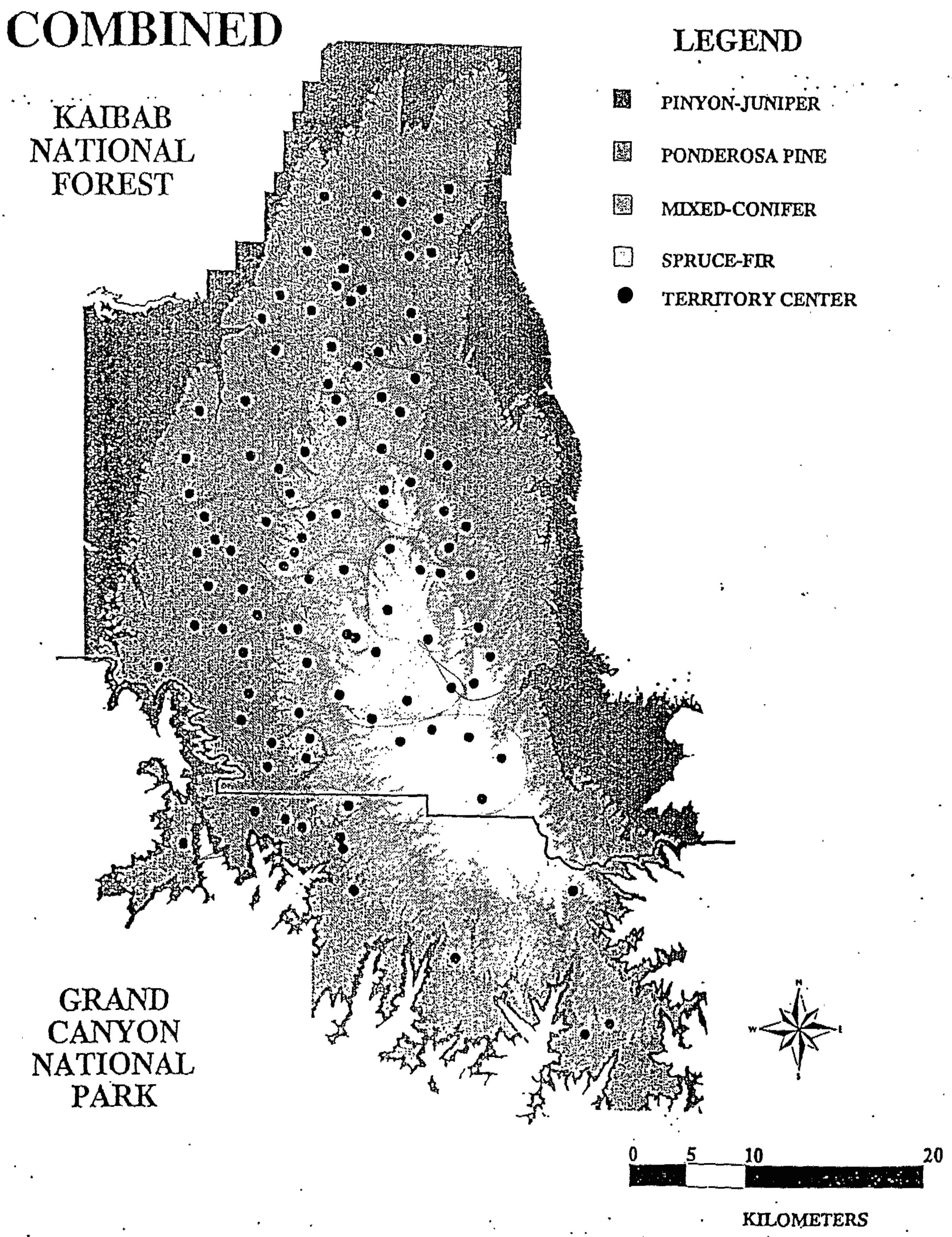

1992
LEGEND
PINYON-JUNIPER
PONDEROSA PINE
MIXED-CONIFER
SPRUCE-FIR
ACTIVE NEST AREA
KAIBAB NATIONAL FOREST
GRAND CANYON NATIONAL PARK
0
5
10
20
KILOMETERS


1993
KAIBAB NATIONAL FOREST
LEGEND
PINYON-JUNIPER
PONDEROSA PINE
MIXED-CONIFER
SPRUCE-FIR
ACTIVE NEST AREA
GRAND CANYON NATIONAL PARK
N
W
E
S
0
5
10
20
KILOMETERS

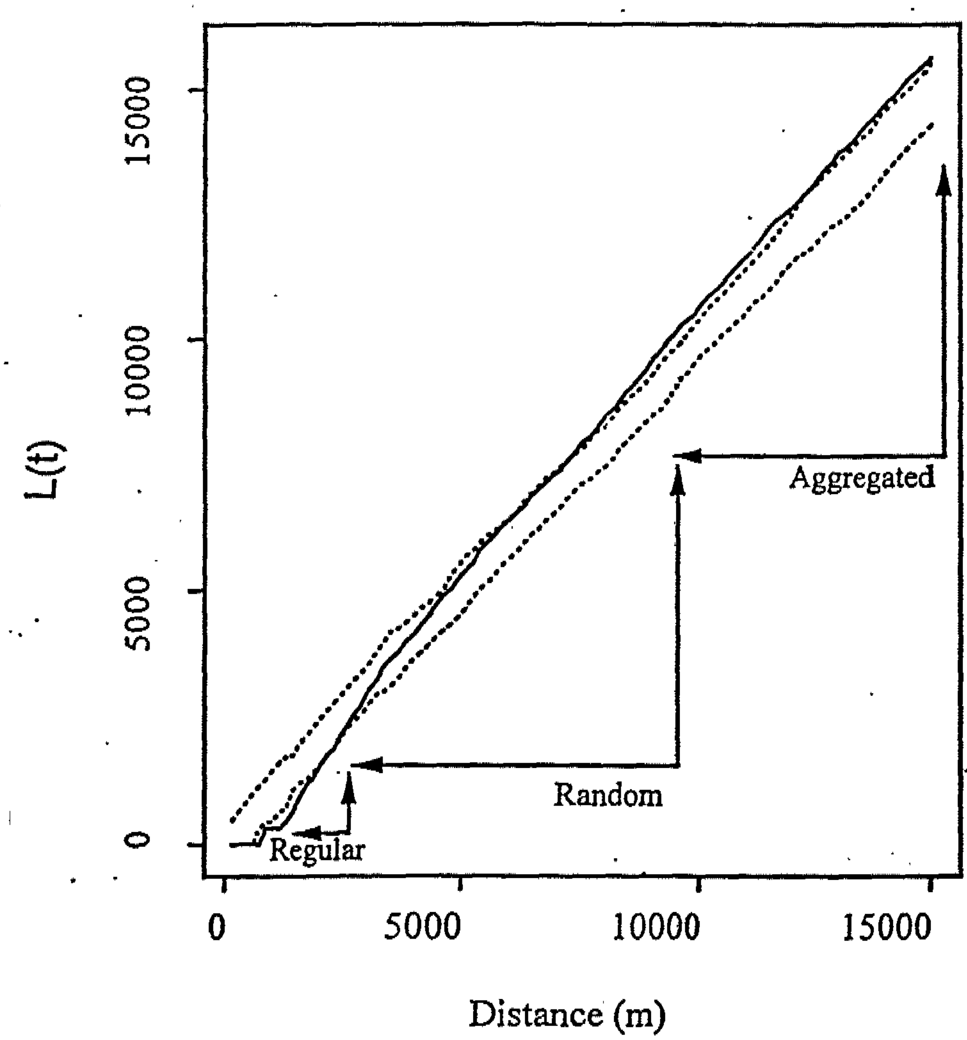

1994
KAIBAB NATIONAL FOREST
LEGEND
PINYON-JUNIPER
PONDEROSA PINE
MIXED-CONIFER
SPRUCE-FIR
ACTIVE NEST AREA
GRAND CANYON NATIONAL PARK
0
5
10
20
KILOMETERS

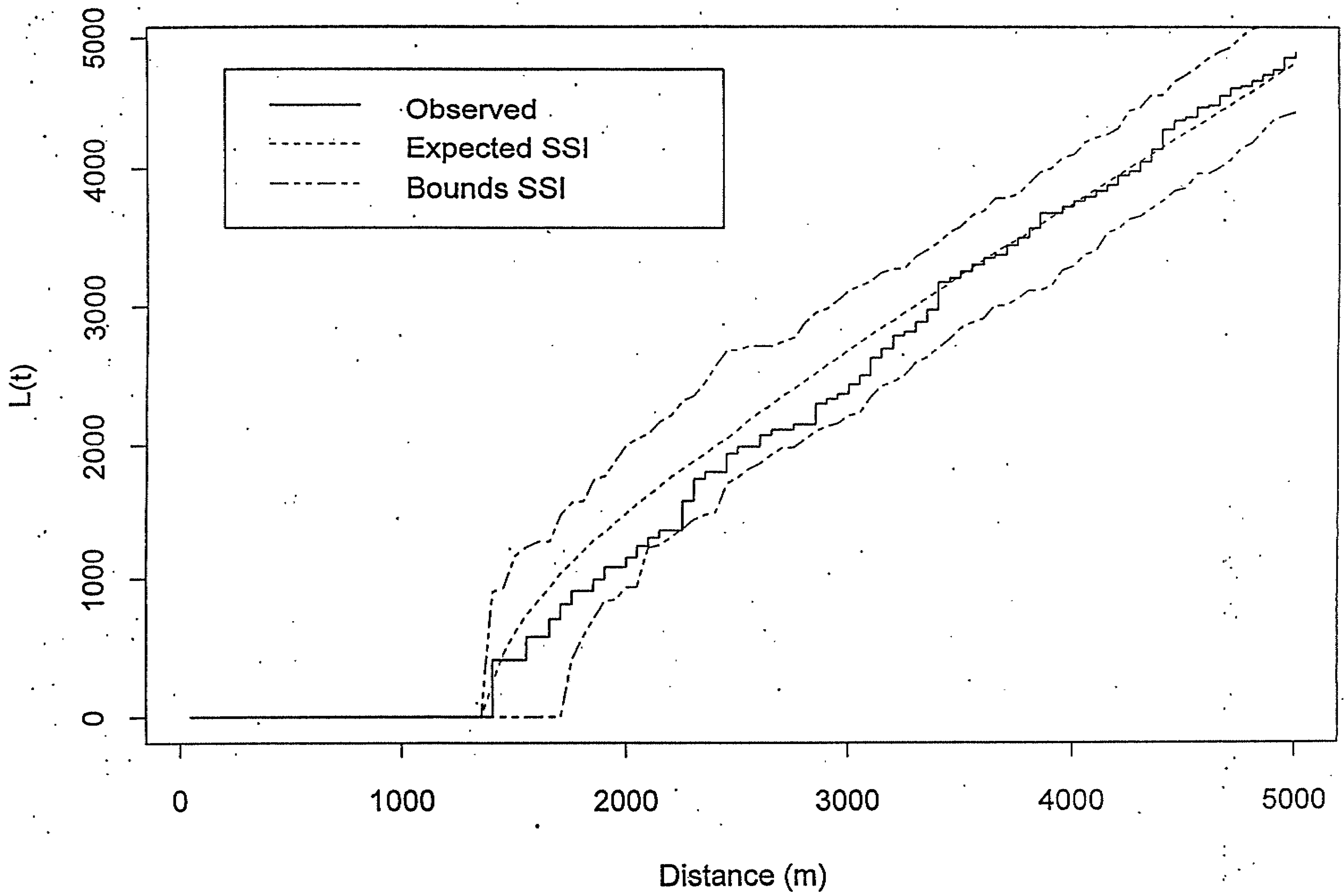

1995
LEGEND
PINYON-JUNIPER
PONDEROSA PINE
MIXED-CONIFER
SPRUCE-FIR
ACTIVE NEST AREA
KAIBAB
NATIONAL
FOREST
GRAND
CANYON
NATIONAL
PARK
N
W
E
S
0
5
10
20
KILOMETERS

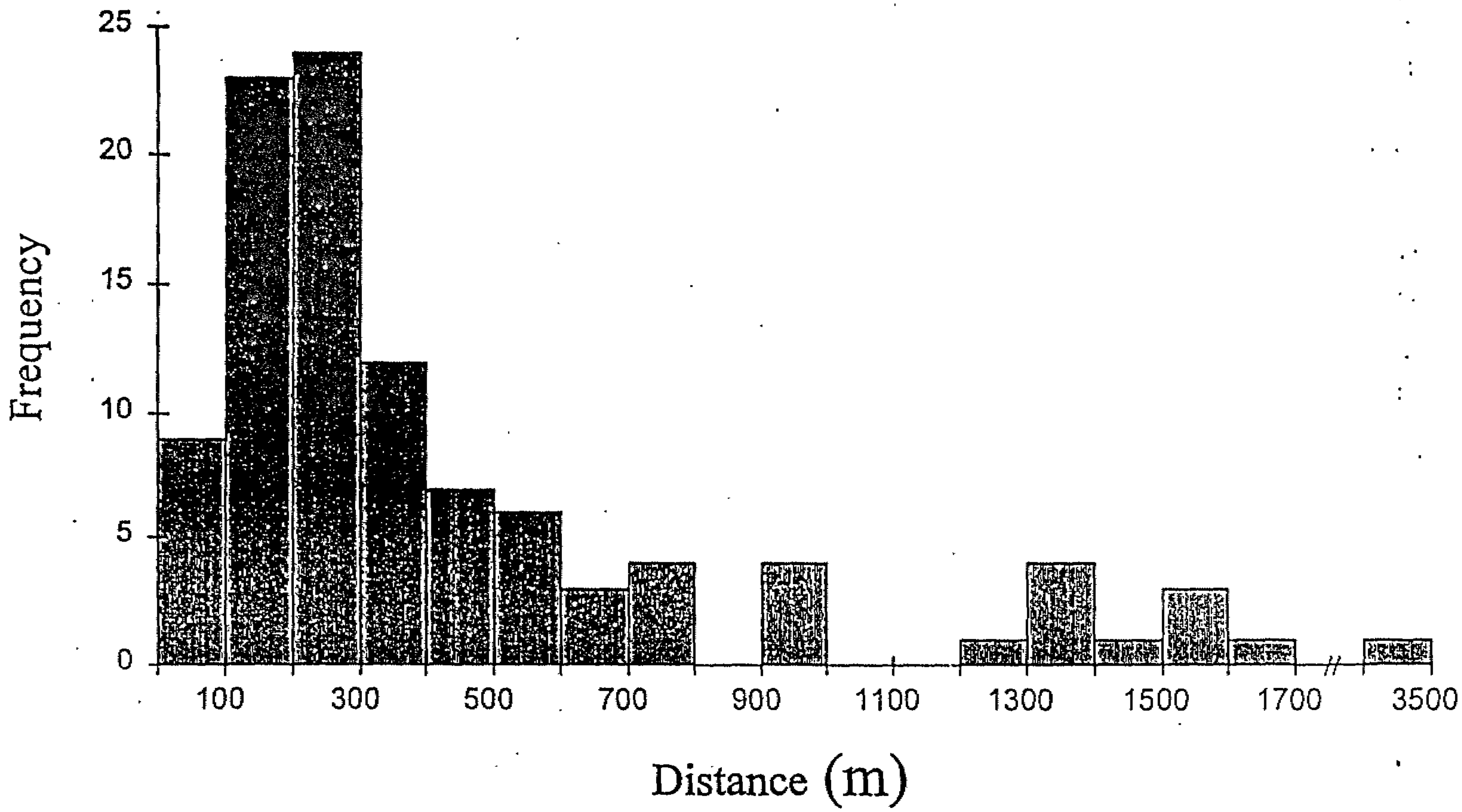

1996
KAIBAB NATIONAL FOREST
LEGEND
PINYON-JUNIPER
PONDEROSA PINE
MIXED-CONIFER
SPRUCE-FIR
ACTIVE NEST AREA
GRAND CANYON NATIONAL PARK
0 5 10 20
KILOMETERS


COMBINED
KAIBAB NATIONAL FOREST
GRAND CANYON NATIONAL PARK
LEGEND
PINYON-JUNIPER
PONDEROSA PINE
MIXED-CONIFER
SPRUCE-FIR
TERRITORY CENTER
0
5
10
20
KILOMETERS

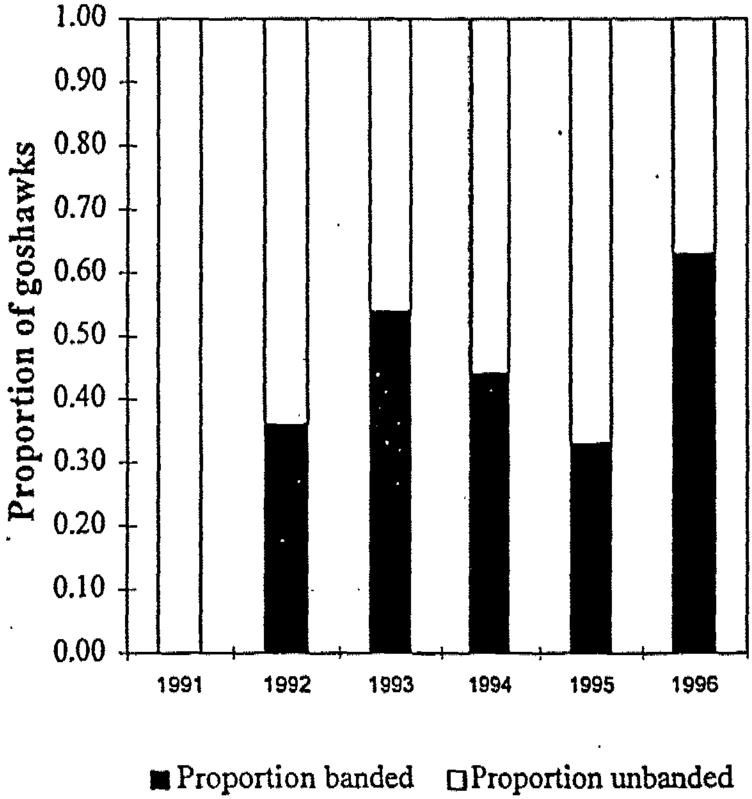
K-function of Goshawk Territory Distribution




Observed
Expected SSI
Bounds SSI
L(t)
0
1000
2000
3000
4000
5000
Distance (m)

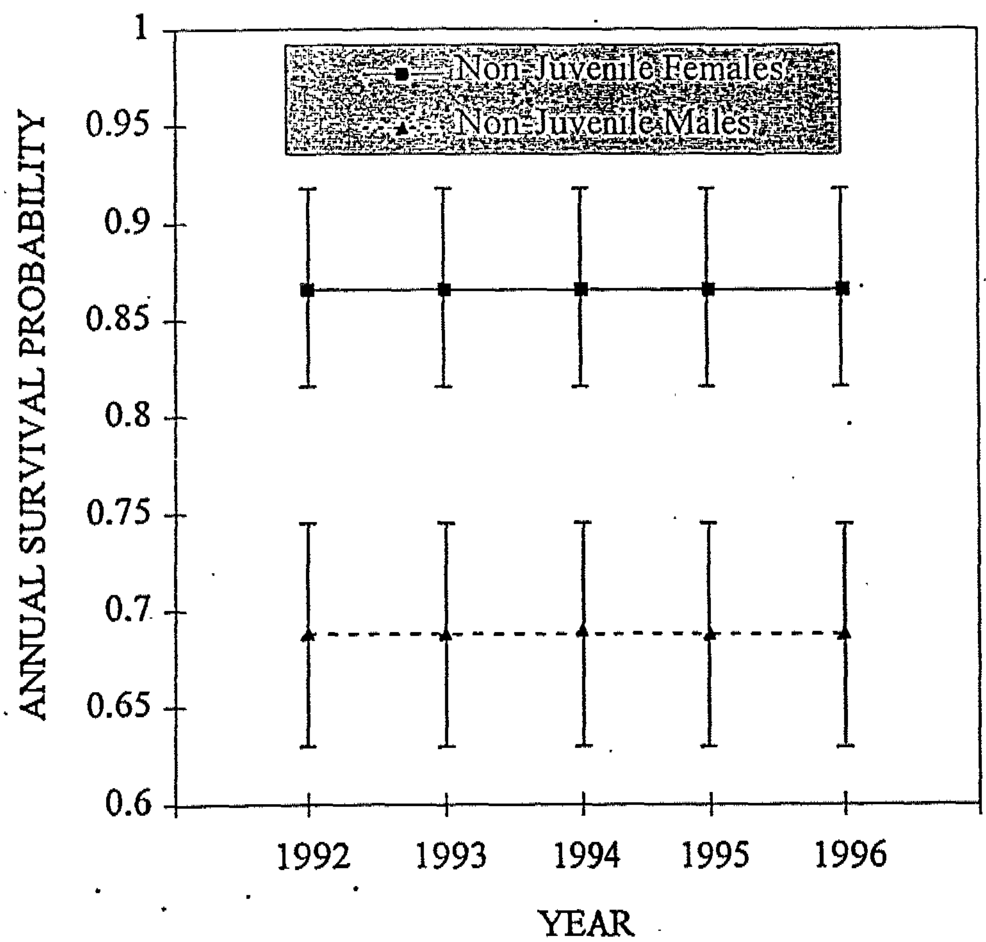


25
20
15
10
5
0
Frequency
100
300
500
700
900
1100
1300
1500
1700
3500
Distance (m)



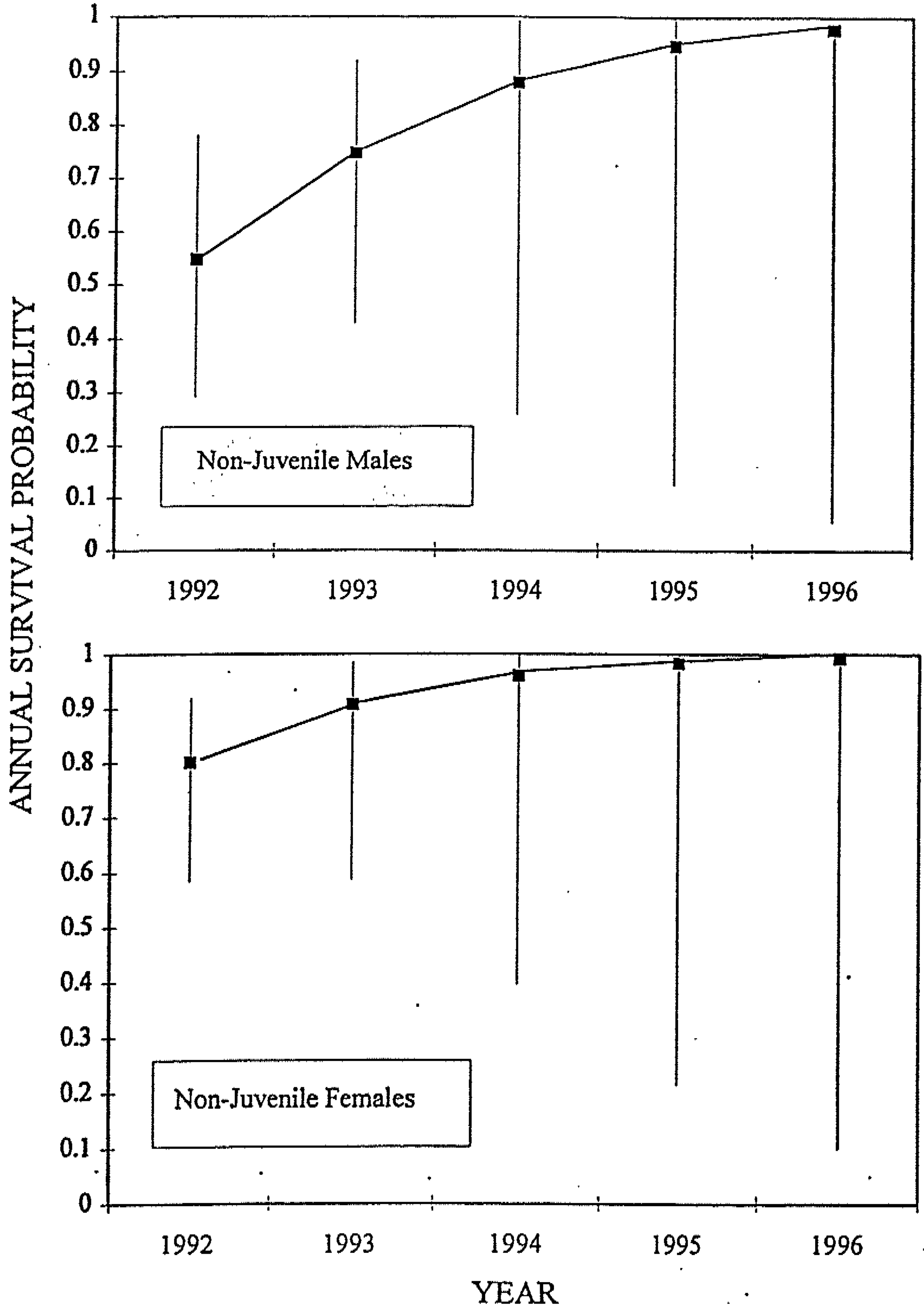
Proportion of goshawks
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
1991
1992
1993
1994
1995
1996
Proportion banded
Proportion unbanded

Phi_s, P_t

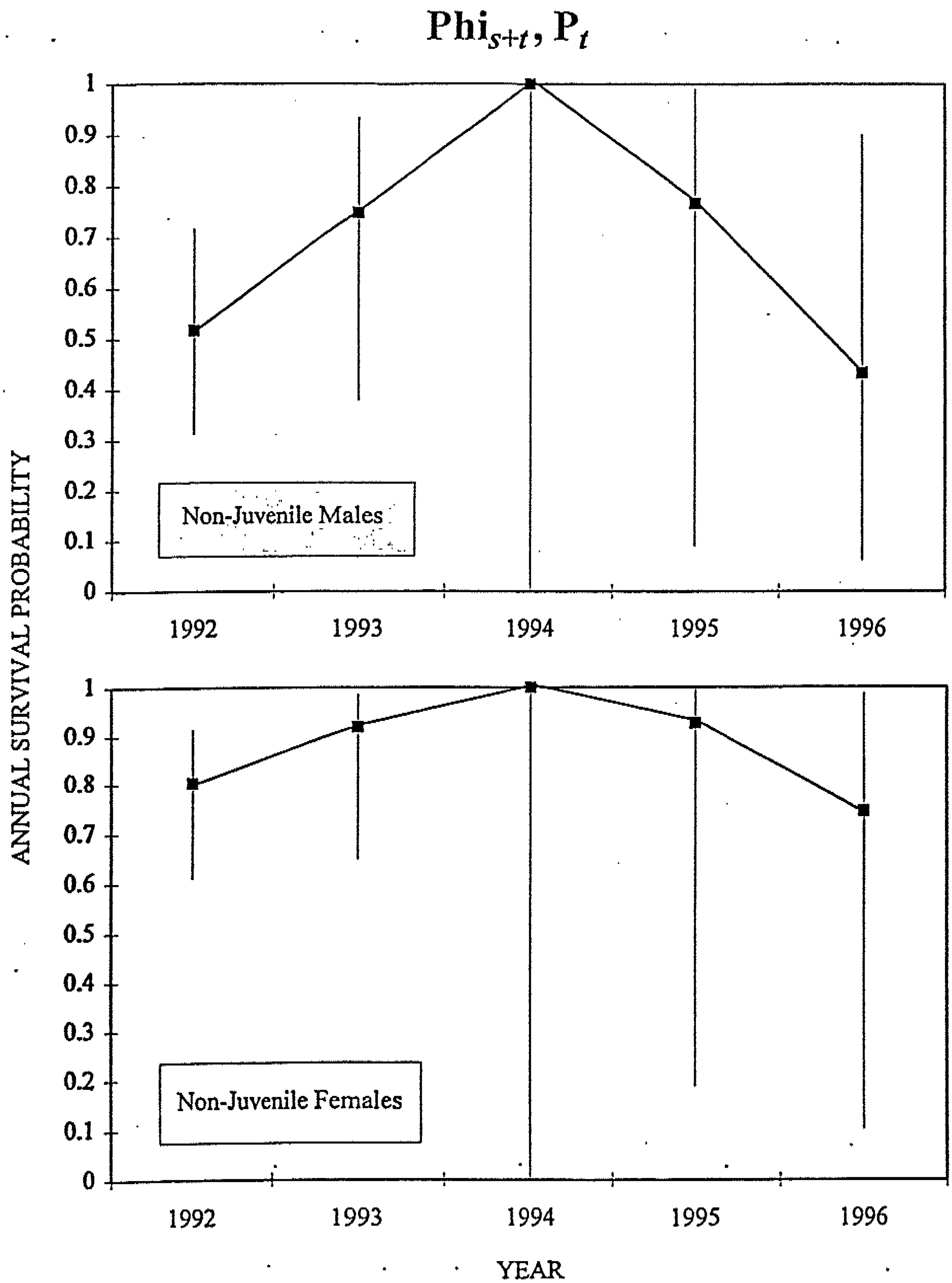


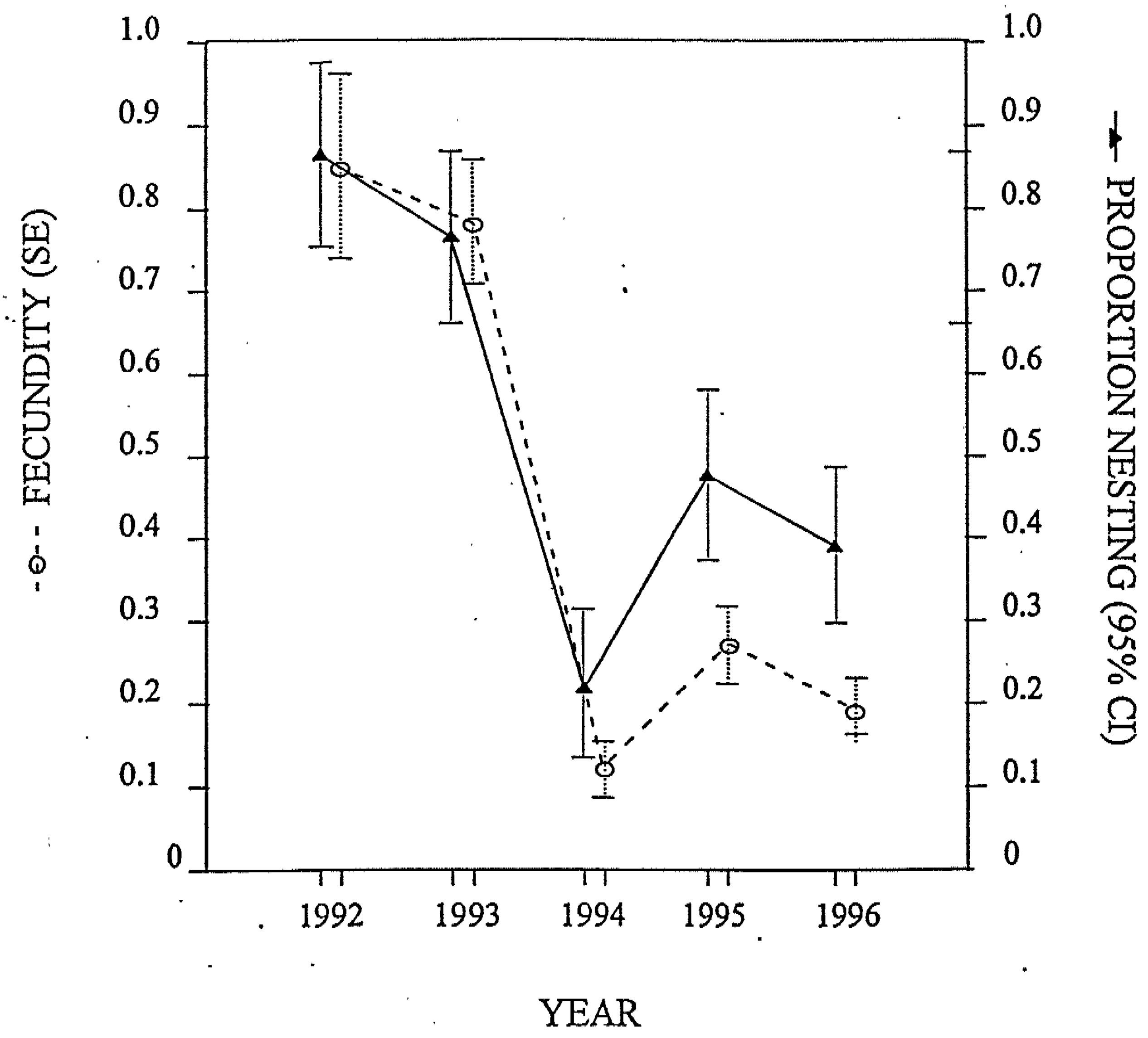
Non-Juvenile Females
Non-Juvenile Males
ANNUAL SURVIVAL PROBABILITY
1
0.95
0.9
0.85
0.8
0.75
0.7
0.65
0.6
1992
1993
1994
1995
1996
YEAR

Phi_{s+T}, P_t

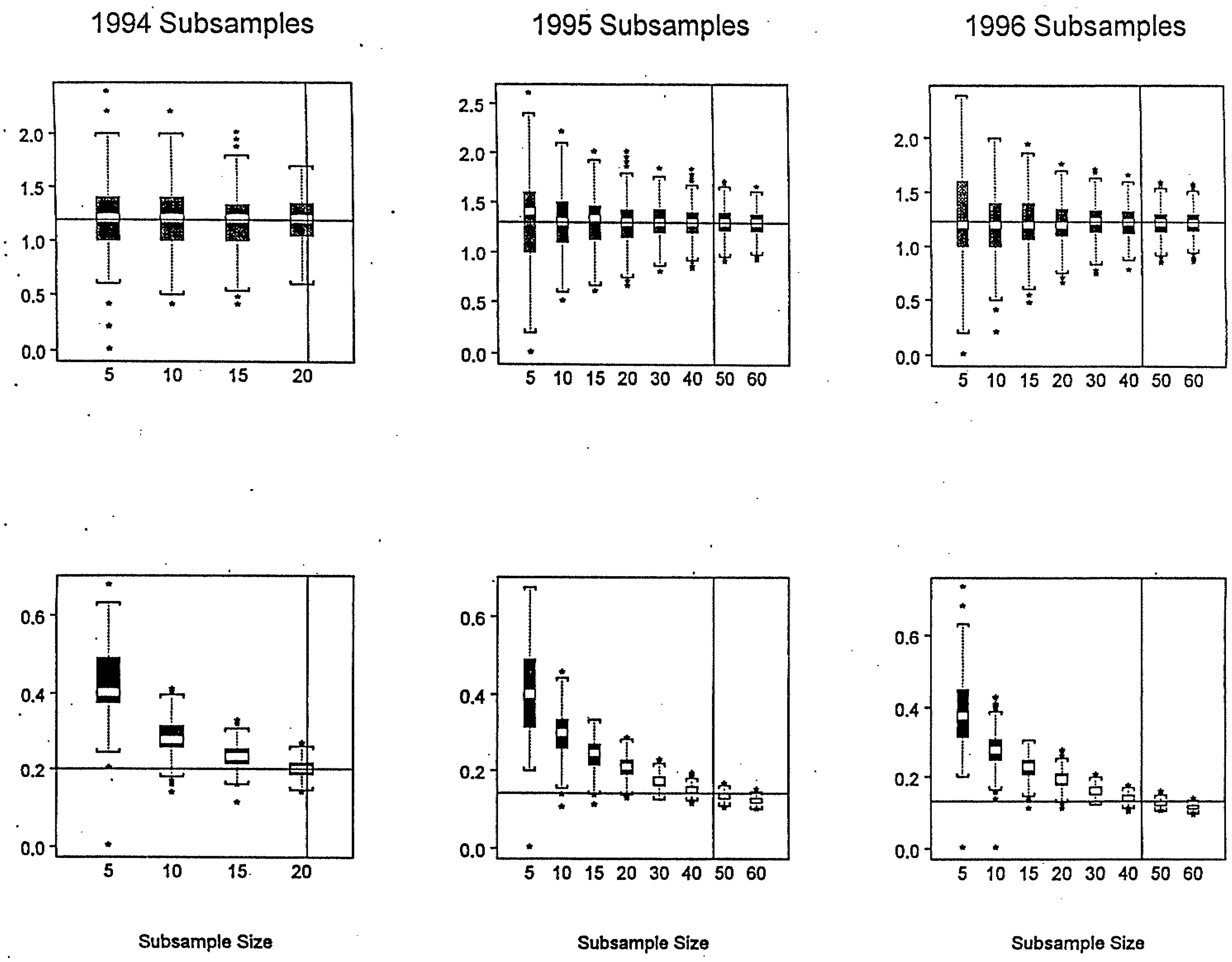


ANNUAL SURVIVAL PROBABILITY
Non-Juvenile Males
Non-Juvenile Females
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
1992
1993
1994
1995
1996
YEAR

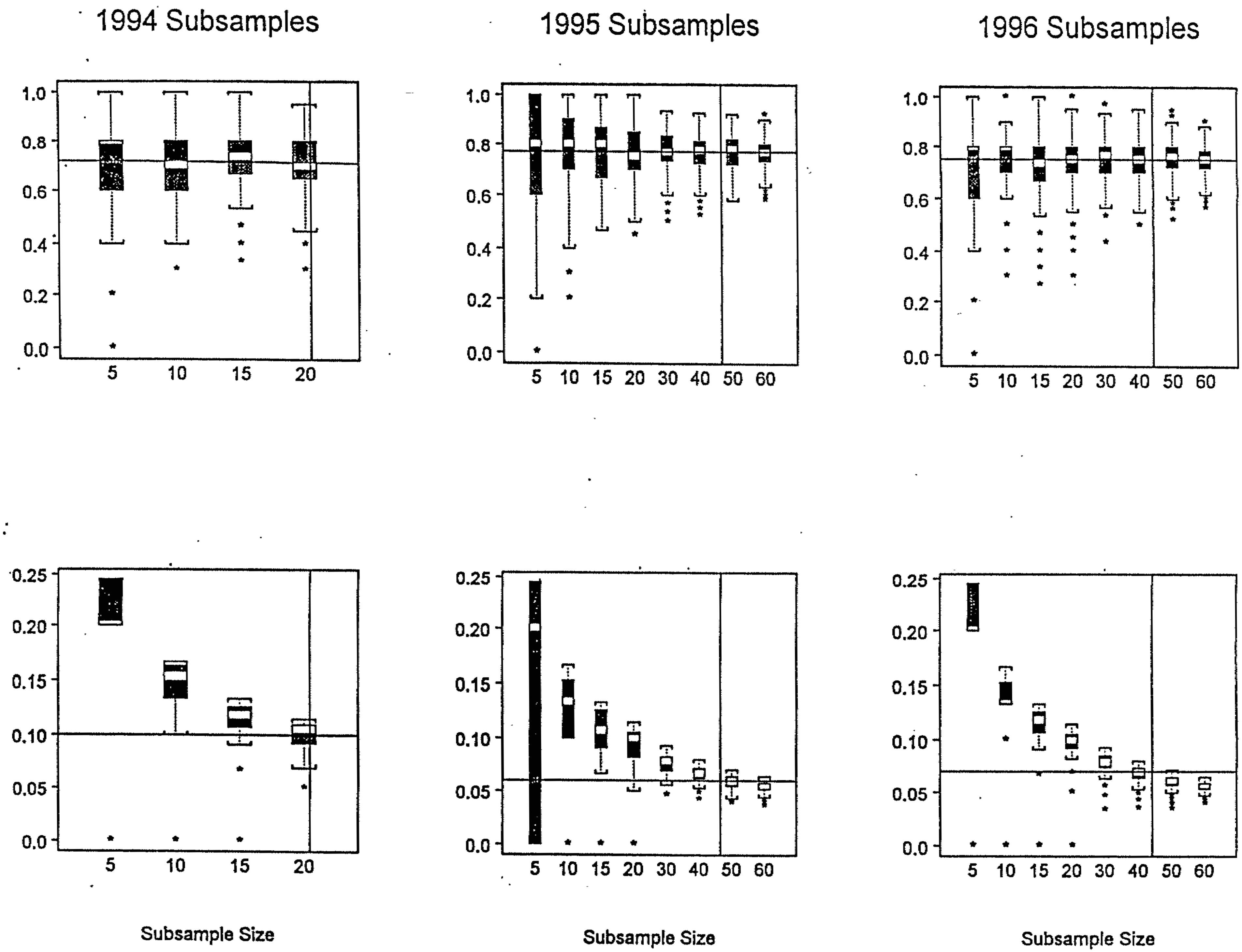

Phi$_{s+t}$, P$_t$
ANNUAL SURVIVAL PROBABILITY
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Non-Juvenile Males
1992
1993
1994
1995
1996
Non-Juvenile Females
YEAR

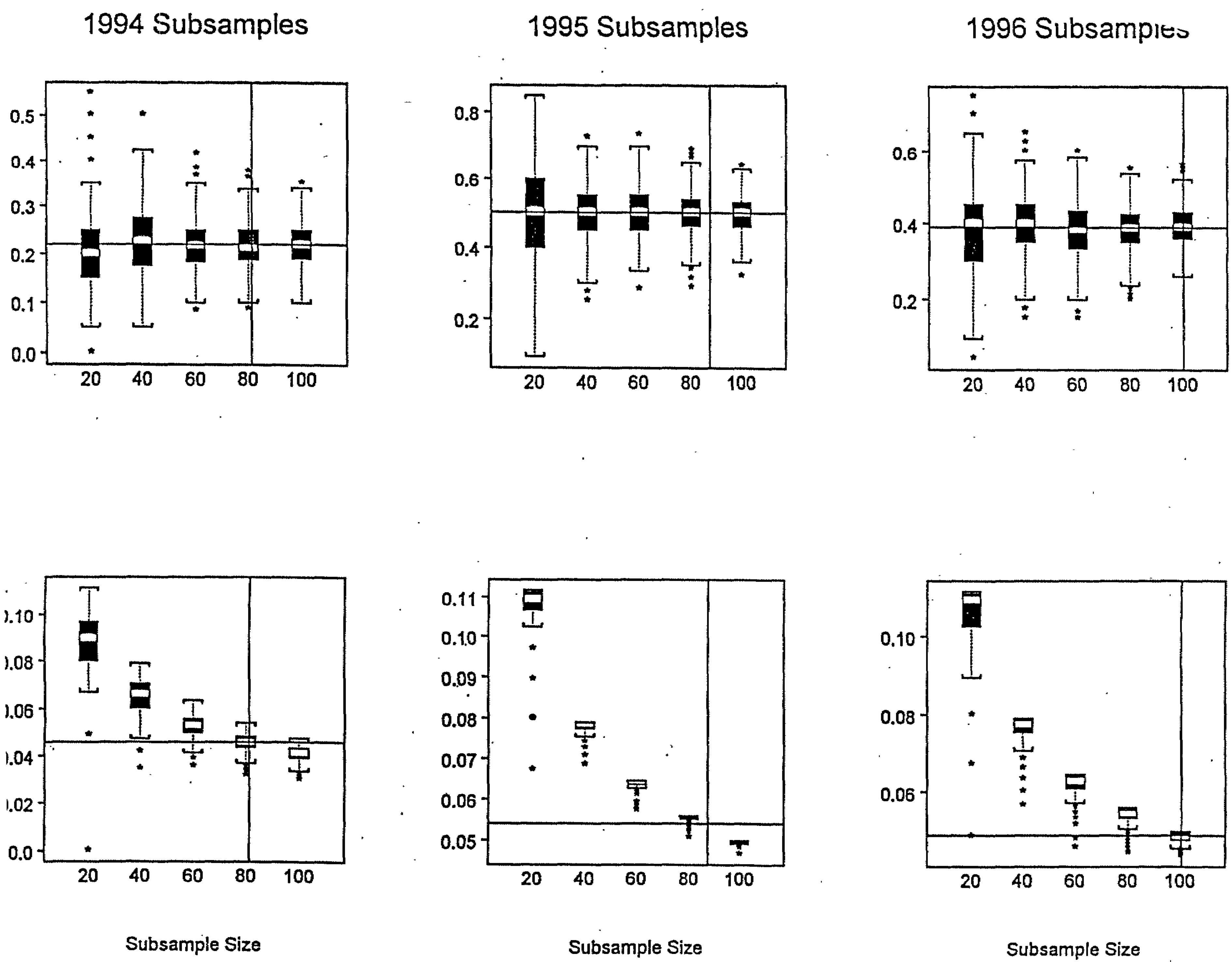


-o- - FECUNDITY (SE)
-▲- PROPORTION NESTING (95% CI)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
1992
1993
1994
1995
1996
YEAR



1994 Subsamples
1995 Subsamples
1996 Subsamples
2.5
2.0
1.5
1.0
0.5
0.0
0.6
0.4
0.2
5
10
15
20
30
40
50
60
Subsample Size


1994 Subsamples
1995 Subsamples
1996 Subsamples
Subsample Size
Subsample Size
Subsample Size


1994 Subsamples
1995 Subsamples
1996 Subsamples
Subsample Size
Subsample Size
Subsample Size

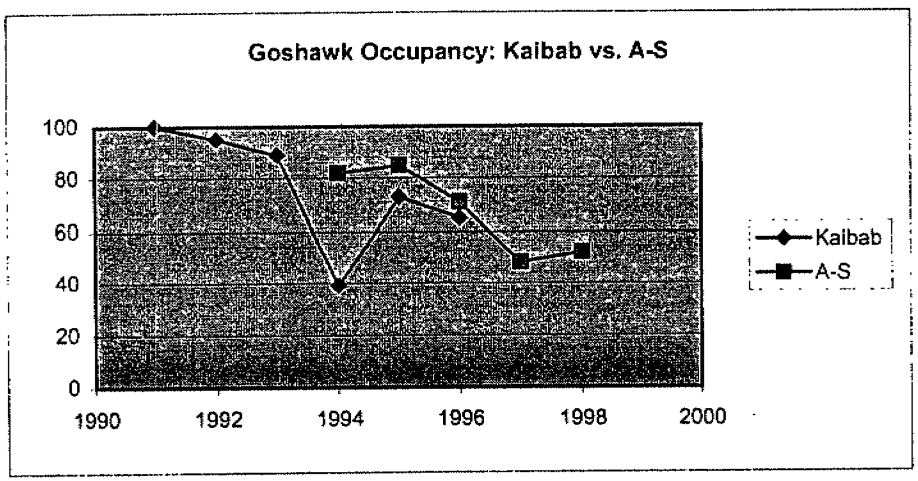
Study	Variable	1991	1992	1993	1994	1995	1996	1997	1998	mean	mean for co
Kaibab	Occupancy	100%	95%	89%	39%	73%	65%	N/A	N/A	77%	59%
A-S		N/A	N/A	N/A	82%	85%	71%	48%	52%	68%	79%
Kaibab	Nesting activity rate	N/A	86.50%	76.60%	22%	48.90%	39%	29%	51%	50.43%	44%
A-S		N/A	N/A	69%	33%	66%	52%	31%	43%	49%	49%
Kaibab	Nest failure rate	N/A	31.30%	18.40%	27.80%	23.30%	25.60%	19%	14%	22.77%	21%
A-S		N/A	N/A	6%	27%	46%	27%	54%	21%	30%	30%
Kaibab	Fledglings/active nest	2	1.8	1.7	1.2	1.3	1.3	N/A	N/A	1.55	1.375
A-S		N/A	N/A	1.66	1.45	1.04	1.27	0.54	1.58	1.26	1.355
Kaibab	Fledglings/successful nest	2.1	2.2	2	1.7	1.6	1.7	1.4	2.1	1.85	1.75
A-S		N/A	N/A	1.76	2	1.93	1.75	1.67	2	1.85	1.8516667

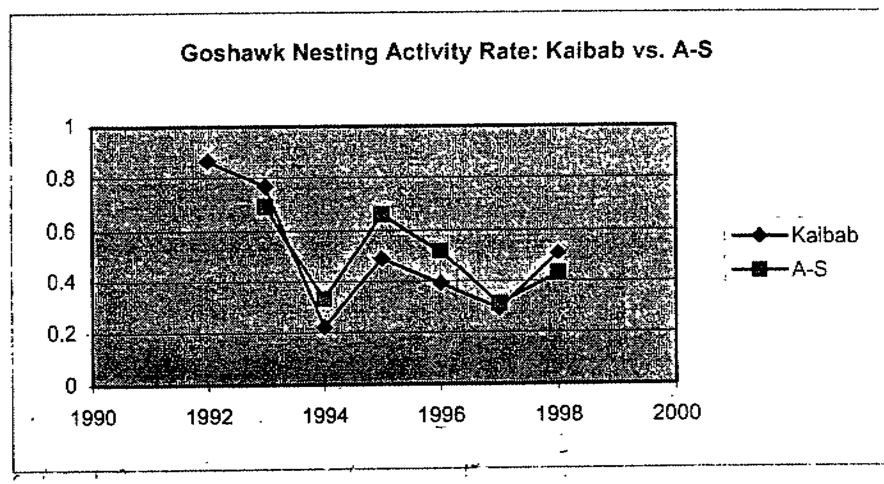
Occupacy

Year	Kaibab	A-S
1991	100	
1992	95	
1993	89	
1994	39	82
1995	73	85
1996	65	71
1997		48
1998		52

Nesting activity rate

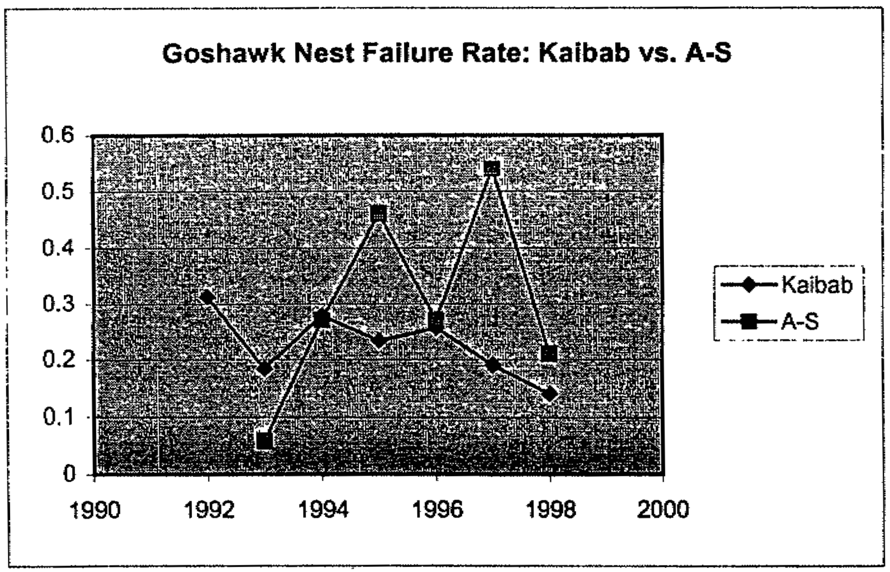
Year	Kaibab
1991	
1992	86.50%
1993	76.60%
1994	22%
1995	48.90%
1996	39%
1997	29%
1998	51%

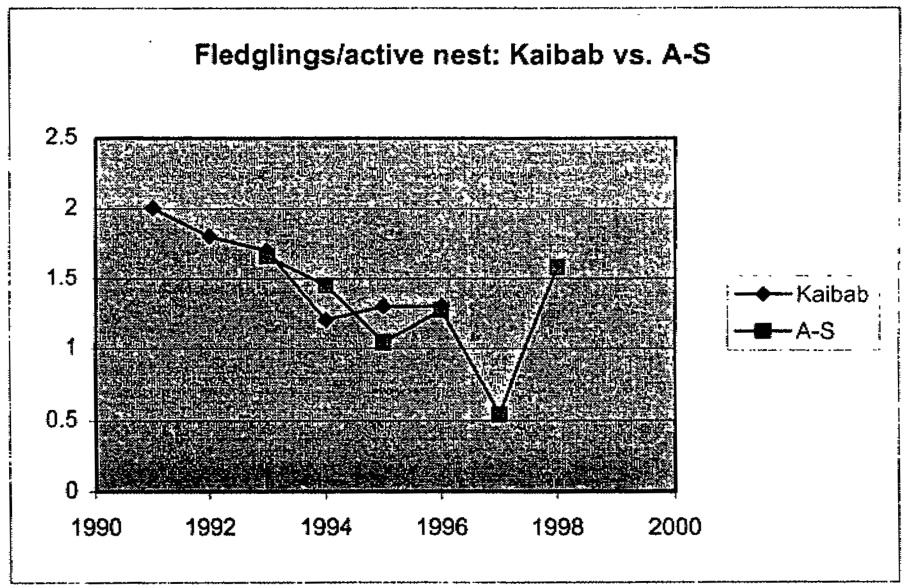




Nest Failure Rate	Year	Kaibab	A-S
	1991		
	1992	31.30%	
	1993	18.40%	6%
	1994	27.80%	27%
	1995	23.30%	46%
	1996	25.60%	27%
	1997	19%	54%
	1998	14%	21%

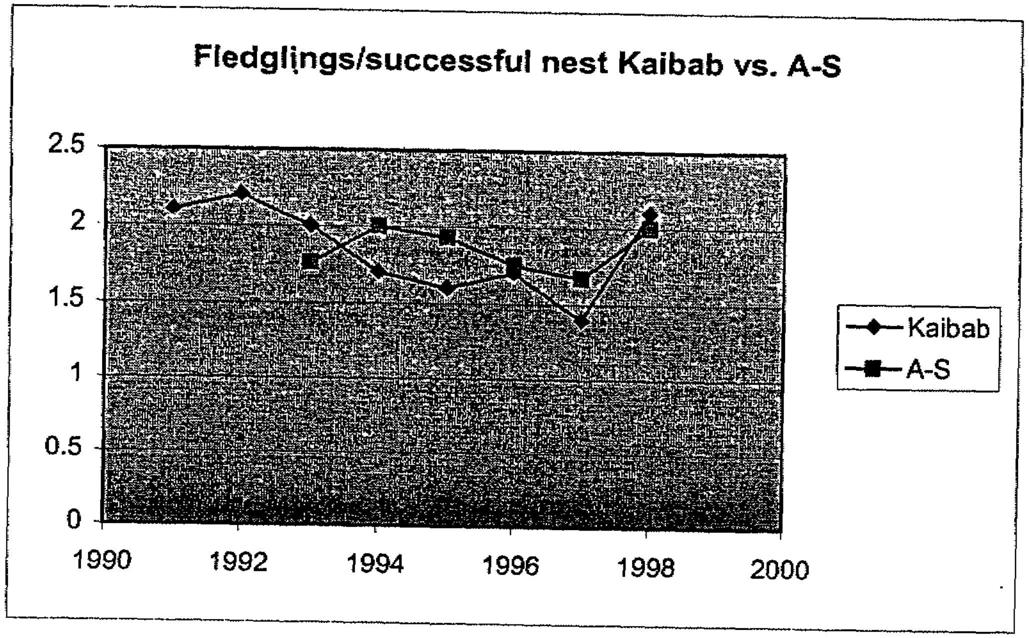
Fledglings/active nest	Year	Kaibab
	1991	2
	1992	1.8
	1993	1.7
	1994	1.2
	1995	1.3
	1996	1.3
	1997	
	1998	

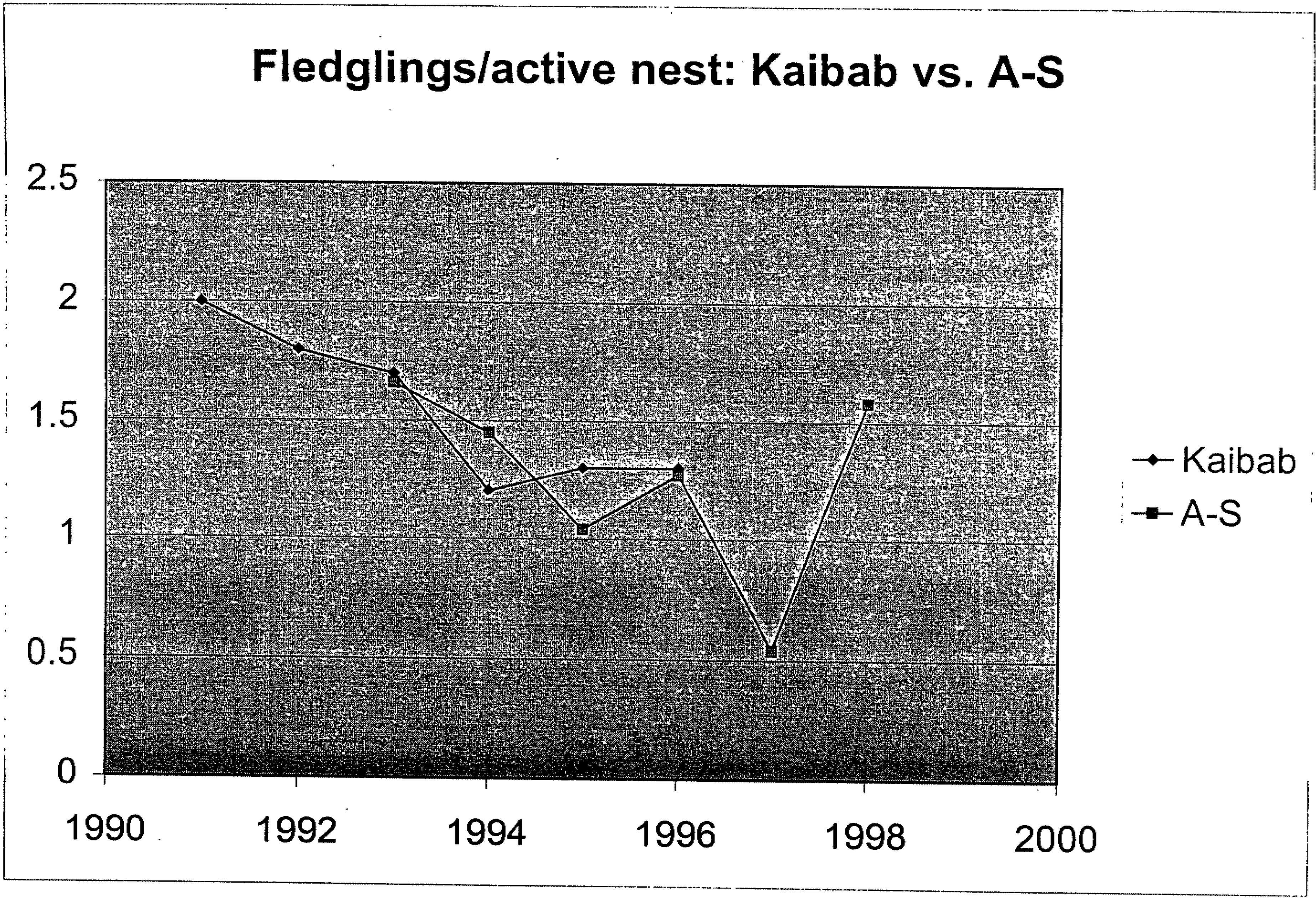




Fledglings/successful nest

Year	Kaibab	A-S
1991	2.1	
1992	2.2	
1993	2	1.76
1994	1.7	2
1995	1.6	1.93
1996	1.7	1.75
1997	1.4	1.67
1998	2.1	2




Fledglings/active nest: Kaibab vs. A-S
2.5
2
1.5
1
0.5
0
1990
1992
1994
1996
1998
2000
Kaibab
A-S